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October 2, 1832—Born at Breslau, Germany.

1845–50—Attended the Gymnasium at Breslau.

1851–56—Student at Karls-Ferdinands Universität, Prag.

1856—Received degree of Doctor of Philosophy from Karls-Ferdinands Universität.

1857–59—Privatdocent at Karls-Ferdinands Universität.

1859–61—Physiological assistant at Agricultural Academy of Tharandt.

1861–67—Professor of Botany and Natural History at Agricultural Academy of Poppelsdorf, near Bonn.

1865—Published 'Handbuch der Experimental-Physiologie der Pflanzen.'

1868—Professor of Botany at University of Freiburg, succeeding De Bary. Published 'Lehrbuch der Botanik.'

1869–97—Professor of Botany, University of Würzburg.

1875—Published 'Geschichte der Botanik.'

May 29, 1897—Died at Würzburg.

LIST OF STUDENTS

First students:

In Bonn—Gregor Kraus In Freiburg—Millardet

In Würzburg—

Baranetzky	Hansen	Reinke
Bower	Hauptfleisch	D. H. Scott
Brefeld	Klebs	Stahl
Fr. Darwin	J. Loeb	Vines
Detlefsen	H. Müller-Thurgau	deVries
Elfving	Moll	Marshall-Ward
W. Gardiner	Noll	Weber
Godlewski	Pedersen	Wortmann
Goebel	Pfeffer	Zimmermann
	Prantl	

PLANT PHYSIOLOGY AS SACHS FOUND IT[1]

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Formative Influences

Julius von Sachs, in whose honor this celebration is held, began his work at a strategic time in the development of plant physiology. The foundational sciences of chemistry and physics had emerged from the restraints imposed upon them by the spirit of the Middle Ages and the bases for many of the modern concepts had been laid. Since the development of modern plant physiology was necessarily dependent upon a scientific understanding of the laws of physics and chemistry the best that could be expected of primitive biological studies was an accurate description of the apparent reactions of organisms. Although the ancients, including the most noted of the philosophers, had a modicum of essentially correct concepts of animal physiology, because of the subjective element in human physiology they failed, due to the objective character of plants, in understanding even as much concerning them as they knew of animals. The nutritional dependence of plants upon their environment, together with a realization that some method of transfer of materials in the plant is necessary, the obvious importance of seeds in the continuity of life and certain empirical observations upon apparent values of certain fertilizing materials—these constituted essentially the stock in trade of the ancients. Later, analogies between the better-known activities of animals, especially of the human body, and the supposed reactions of plants resulted in the accumulation of certain hypotheses which, although unsupported by experiments or adequate observation, have in some instances more recently been demonstrated as correct. These, however, were scarcely more than lucky guesses. It is true, nevertheless, that progress in animal physiology has often been of great value in suggesting profitable lines of investigation

[1] A paper read at the celebration held at the Missouri Botanical Garden, December 27, 1931, in honor of the one-hundredth anniversary of the birth of Julius Sachs.

in the physiology of plants. During the history of our science there has been an interesting oscillating from the extreme of the complete dependence upon analogies with animal physiology, of the ancients, to the opposite extreme, as exemplified by Schleiden (1849), who refers to "the fanciful analogy between the physiology of animals and of plants." "In consequence," he continues, "of the use of this absurd analogy, almost all of the works which have hitherto appeared on vegetable physiology are perfectly worthless, for in no instance have they adopted the only true fundamental position, namely, the essential peculiarity of vegetable life." The pendulum was to swing back, due in no small measure to Schleiden's further studies, to a recognition of the essential unity of life, together with a proper regard for its numerous modifications and diversities. Not only did advances in animal physiology aid in establishing a point of view in the study of plants, but two other influences also were of prime importance in giving a proper impetus to the formation of a true science of vegetable physiology.

Developments in general microscopy soon brought more sharply into view the problems of plant structure. Malpighi and Grew, beginning in 1671, illustrated and carefully described much of the tissue structure of plants, although it seems clear that they did not conceive of these organisms as built up of the unit structures now known as "cells"; nor was it until von Mohl, about 1830, a hundred and fifty years later, clearly expounded the proposition that the cell is the unit of structure, that there was a general acceptance of this doctrine. Nevertheless, the exact knowledge of the general anatomy of the stem led to numerous queries as to the utility of the various units to plants. Thus a fairly correct understanding of anatomy stimulated a study of physiology. Malpighi had concluded that the leaves of plants are important in their nutrition, and before that von Helmont's famous experiment with the willow tree had demonstrated the fallacy of the ancient belief that elaborated food from the soil is the chief source of plant substance. Yet as late as the publication of Schleiden's and von Mohl's texts, it was found necessary to controvert vigorously this belief in the absorption of large quantities of organic food from the soil.

Stephen Hales in 1727 published his 'Vegetable Staticks,' and as this was the first considerable attempt to study plant physiological problems by exact measurements it is especially important in examining the bases of the modern science. Among the phenomena studied were transpiration, the pulling action of leaves on the transpiration stream, the reduced pressure in the plant during active transpiration, stump pressures, pressures developed in spring vegetation, the alleged circulation of sap, presence of air in stems, the free passage of water in either direction through the stem when leaves are actively transpiring, and the rate of passage of water upward due to leaf pull contrasted with the downward movement under the weight and pressure of several feet of water. In many of these problems he came to essentially correct conclusions and remained for a hundred years the brightest light in the field of the application of physics to vegetable physiology.

Robert Brown, about 1833, is credited with having discovered and named the cell nucleus, the movement of protoplasm, and most important, from the theoretical physiological aspect, the dancing movement of small particles suspended in liquid which was named for him the Brownian movement.

It is to the rapid development of chemistry, however, that we must look for the main stimulus which finally established plant physiology upon a modern scientific basis. Just before the elimination of the phlogiston theory in chemistry, Priestley (1790), in the course of his studies upon atmospheric gases, published a series of studies upon the relations of plants to the air. Some of the section titles of his work, giving an indication of his contributions to the subject, are as follows:

"Of the Restoration of Air, in which a Candle has burned out by Vegetation."

"Of the Restoration of Air infected with animal Respiration or Putrefaction, by vegetation."

"Of the Growth of Plants in dephlogisticated Air."

"Of the State of Air confined in the bladders of Sea Weed."

"Of the spontaneous Emission of dephlogisticated Air from Water containing a vegetable green Matter."

"Of the Purification of Air by Plants, and the Influence of Light on that Process."

Sachs (1906), in his 'History of Botany,' says: "The establishment of the fact, that parts of plants give off oxygen under certain circumstances, did little or nothing to further the theory of nutrition; and that was all that vegetable physiology owes to Priestley." It seems to the writer, however, that, in view of the above quoted section titles, this dismissal of Priestley with such faint praise is hardly justifiable if one reads carefully his publications. He established the facts that light is essential to the process of giving off oxygen and that in the dark there is definite injury to air, viewed from the point of view of the phlogiston theory. Sachs is further in error when he says later: "Priestley himself did not suspect that the deposit in question, afterwards known as Priestley's matter and found to consist of Algae, was a vegetable substance."[1] He not only "suspected" that it was a "vegetable substance" when he first saw and experimented with it, but in his Section VII definitely states that other scientists better versed in botany had examined it for him and had determined it as a plant; and he finally says he is convinced that it is a plant which reached the jars through its "seeds" either having been in the water to begin with or, floating in the air, had entered due to loose stoppers. He criticized Ingen-Housz even for hypothesizing a spontaneous generation of the plant, rather than accepting the origin through outside infection.

Ingen-Housz (1779), however, published a much more extended study of the whole problem in his 'Experiments upon Vegetables' in which he demonstrated the use of carbon dioxide as the source of carbon for plant nutrition, and the relation of light and the green color of plants to the process. He also stated clearly that atmospheric oxygen is necessary for continued life in plants. Senebier (1800), and especially de Saussure (1804), added much to the preciseness of the chemical demonstrations of the relationship of plant nutrition to carbon dioxide and water and of respiration to the atmospheric gases. Studies of the mineral content of plants and of the source of the nitrogen used by plants completed a reasonable chemical foundation on which new advances could be built. However, much of this new material was either not accepted or at any rate had not become generally

[1] Sachs seems not to have referred to Priestley's publication of 1790.

diffused among botanists until the beginning of Sachs's investigations.

The Status of Plant Physiology in 1850

With this brief review of the main sources of stimulation for the establishment of a science of plant physiology we may now turn more particularly to the status of the subject when Sachs appeared in the field. It is convenient to select the year 1850 as approximately the end of the pre-Sachs period, especially because at about this time von Mohl (1852) published his 'Principles of the Anatomy and Physiology of the Vegetable Cell,' which indicates especially well the status of the subject at that period. A short time before this Schleiden's (1843) 'Grundzüge der Wissenschaftlichen Botanik' had appeared, and this also presents a picture somewhat different from von Mohl's summary. The term "protoplasm" had just been accepted, but there was no clear understanding of the usual process of cell formation, as is indicated in this statement by Schleiden (1849): "The process of the reproduction of cells by the formation of new cells in their interior is a general law in the vegetable kingdom and is the foundation of the production of cell-tissue." Nevertheless, the importance of a clear understanding of the process was clearly recognized in his further statement that "The question respecting the multiplication of the cells consequently includes the origin and the life of the whole plant, which remains altogether obscure to us previous to the elucidation of this relation."

The group of catalysts had been recognized and named by chemists; and the general catalytic action of the "slime" or "protoplasm" had been discovered. These observations led finally to the recognition of specific catalytic action in plants. Thus Payen and Persoz in 1833 had named diastase and had cleared up some of the earlier misunderstandings concerning the changing of starch to sugar; and Liebig and Wöhler had recognized and named emulsin in 1837 as a substance acting upon amygdalin. Still the significance of these enzymes as representatives of a class of substances was not appreciated, and the conditions governing their activities were not well understood. Nevertheless, a few foundation stones for a study of enzyme chemistry had been laid.

Following the early observations by Nollet and others, Dutrochet, about 1830, developed the concept of endosmosis as an explanation of absorption by the plant, and thereafter a general extension of the theory of endosmosis offered an explanation of the passage of water from cell to cell throughout the parenchyma tissues. However, no careful quantitative determinations of pressures were made and the theories were vague. Thus von Mohl (1852) says: "Since the discovery of endosmose, most vegetable physiologists have assumed it as an axiom that the absorption by cells depends wholly and solely upon the laws of endosmose, none of the peculiar forces of the living cell co-operating. All the conditions to bring about strong endosmosis do really exist in the living vegetable cell, namely, a membrane freely penetrable by watery fluids; on the one side of this the cell-sap which contains proteine substances, dextrine, sugar, etc., in solution, on the other side the water occurring in nature, in the state of an extremely diluted saline solution. This renders it readily explicable how cells which are laid in water swell up rapidly, in many cases, if they contain a concentrated protoplasm and have not firm walls (e.g., many pollen-grains), the powerful absorption of water causing them to burst; and how, on the other hand, if they are laid in a strong solution of sugar, gum, etc., they become emptied and collapse. Under these circumstances, the assumption that the absorption of the cells will be regulated by the laws of endosmose, is fully justified, yet special proofs of this can only be partially advanced, because on one side the phenomena of absorption are too little known in many respects, and on the other side the theory of endosmose is not yet perfect enough to allow of our making out in all cases the share it has in any given phenomenon." The limitations of the term "endosmosis" were not clear and even yet there is a lack of clarity in the usage of terms and the concepts included. For example, osmosis is sometimes still made to include the passage of both solute and solvent through the membrane, which at that time was believed to be the cell wall, although there are obvious advantages in restricting the term to the diffusion of the solvent and thus recognizing the process as a special case of diffusion in which pressures are developed and maintained. The diffusion of

solutes then falls into its place as an example of the general process.

The universal solvent action of water for all substances, including gases, entering the plant was well recognized. Quantitative determinations of the mineral content of plants had been made, which indicated the relatively small quantities necessary and the range of salts usually present. These data had also indicated a problem less easily explained, however, namely, why several kinds of plants living upon the same soil may accumulate different proportions of the various soil solutes. Liebig's hypothesis of excretion was offered by him to account for this phenomenon by assuming no differential permeability but a subsequent excretion of supposedly toxic mineral substances. Later, the experiments of others indicated differential absorption.

The problem of transportation in the plant was in an active state of discussion. The older vegetable anatomists, Malpighi and Grew, had studied the vascular system and described the elongated tubes as "tracheae" which, so far as they could detect, always contained air. Others, through unconvincing experiments, had stated that these tubes were the water-conducting channels. Schleiden (1849), in various portions of his 'Principles,' called attention to the incomplete nature of the evidence, and his conclusions are clearly indicated thus, "That the vessels convey only air, and no juices, may be seen by any one possessing the least physical knowledge, on the most cursory glance at a longitudinal section of a plant"; and again, "The so-called vessels in most plants never convey sap; and with others it is probable that they convey it only during a few weeks while the new buds are forming." He inclined toward the belief that all transfer of fluid in plants was from cell to cell by some osmotic process, but admitted a possibility that at certain seasons of the year in some plants, or under pathologic conditions, sap might pass into and possibly through the fully formed tracheae.

An example of the necessity of a clear differentiation between the solute and the solvent in discussing the subject of sap transfer is seen in the following statement from von Mohl (1852): "All these explanations of the movement of the sap bear reference only

to its ascent, not one of them applies at all to the descent of the elaborated sap. If the bark and the cambium layer attract the nutrient matter from the leaves because their cells contain a more concentrated sap than the cells of the leaves, it is not evident why they cannot draw the sap directly from the root and the wood, instead of by the long circuit through the leaves, and why the bark is wholly incapable of carrying sap upwards." It must be remembered that von Mohl in 1852 was inclined to believe that the passage of water upward must be in the parenchyma cells of the wood by the power of endosmosis induced by transpiration from the foliage, and that there is a corresponding down stream in the bark. In the above quotation, then, there would have been no special problem had he clearly discerned that, on the basis of diffusion, the passage of solutes from cell to cell must be from regions of greater to those of lesser concentrations and that they must move independently of the direction of the solvent.

Transpiration is one of the activities of plants which was recognized by early observers and studied somewhat thoroughly by Hales. The rates and total amounts of water loss were determined for a fair range of representative plants and environments so that the essential unity of transpiration and physical evaporation had been accepted. Schleiden believed that transpiration by concentrating the sap in the leaf cells caused a progressive concentration of sap downward and thus furnished, together with the osmotic action of cells, an adequate explanation of the passage of liquids upward. Guttation was known in some cases and the specialized structures through which it takes place had been studied carefully.

The more common of the mineral elements which are considered as essential to plant growth had been studied; and considerable knowledge of specific chemical compounds from plants had accumulated. The uniformity of certain types of compounds, especially of sugar-like nature, had suggested some nutritional importance for them. The four classes of compounds, carbohydrates, not yet so named, organic acids, oils, and proteins had been distinguished.

As already indicated, the essential outline of photosynthesis

had been drawn but not all of the demonstrations had been fully accepted, and the term respiration still frequently included all gaseous exchanges by plants although von Mohl pointed out the desirability of using it in the restricted sense used in animal physiology.

Ammonia and its salts supplied through the roots appeared to be the main if not sole source of nitrogen, while the free nitrogen of the atmosphere had been ruled out of consideration by the work of several investigators. Although it was considerably later that the nitrifying power of soil organisms was offered as an explanation of the renewal of nitrogen in the soil, and it was believed that the continuous supply of nitrogen for plants was through the ammonia of the atmosphere, still some believed in a slow automatic ammonification in the soil.

The curious milk-sap theory of Schultz (1823–41) is an example of the extremes to which a theorist may go. He supposed that milk-sap was the exact analogue of the blood of animals and claimed that circulation, coagulation, and blood corpuscles were all duplicated in the phenomena which he observed in the milk tubes. This concept was sufficiently important for von Mohl to devote considerable time and argument to demonstrate its fallacies. Schleiden, in a characteristic passage, thus disposes of the older work: "On the subject of these structures, and especially the milk-vessels, I am rather afraid of saying too much than too little, for owing to the total neglect of a correct, scientific method and the purile sporting with hypotheses, without any foundation or guiding principle, the question respecting them is loaded with such a heap of nonsense that the best way in beginning upon it is, in the first place, to throw overboard all that has hitherto been done and commence entirely *de novo*, instead of undertaking the thankless task of cleansing this true Augean stable." The obvious nutritional difference between fungi and green plants had been studied experimentally to some extent from the time when it was demonstrated that the fungi did not absorb carbon dioxide in the light.

An interesting concept of Schleiden concerns the place in which elaboration of the nutritional substances occurs. He believed that the water and its inorganic salts and other necessary sub-

stances become elaborated in each cell so that, as he remarked, "nothing remains for the leaves to assimilate." Thus it was not necessary to have a means of transfer of food substances from the leaves to other parts of the plant and he denied any downward flow of sap in the bark. He appears to have believed that the carbon dioxide absorbed by leaves is conducted through the internal atmosphere to all parts of plants. Thus he says, "The conclusion that the carbonic acid found in the leaves is consumed by them is about as rational as the inference would be, from the respiratory movements of the nose and mouth, that the brain performed the functions of the lungs."

Schleiden lists as one of the main problems of seed germination: "An accurate determination of the degree of heat present during germination and a comparison of the same with the quantities of carbon and hydrogen which are consumed." Von Mohl clearly indicated the rapid loss of sensitivity and subsequent early death of plants cut off from an oxygen supply, thus calling attention to the close analogy between animal respiration and that of plants. The heat produced by plants was directly associated with the respirational process. The modern interpretations of gaseous exchanges between the plant and the atmosphere were not fully accepted at this time although it was known that carbon dioxide provides the carbon supply for green plants. Schleiden, however, stated in 1849 that, "It would appear that the exhalation of oxygen and the absorption of carbonic acid gas never stand in immediate relation with each other," and he saw in the exhalation of carbon dioxide only the beginning of decay. On the other hand, von Mohl, in his 'Anatomy and Physiology of the Vegetable Cell' published in 1852 clearly distinguished between the nutritive and the respirational processes involving the atmospheric gases.

A "fermentation-fungus" had been discovered and it had been suggested as the cause of the process of fermentation, but there was still no clear recognition of the essential nature of the yeast organism and its relation to the fermentation process.

The three main phases of the growth process, cell formation, cell enlargement, and cell differentiation, had been distinguished, but the details of these processes had yet to be filled in.

Due to the almost slavish adherence to the doctrine that all processes in animals must find their exact equivalent in plants, efforts were constantly made to demonstrate a method of excretion which would rid plants of injurious substances. Liebig believed that this was accomplished through the roots, at least to a considerable degree. Others, as, for example, von Mohl, pointed out that no experimental data had been adduced to provide for any but insignificant quantities of substances. A doctrine at that time which was used to uphold the excretion hypothesis taught that there must be an exosmosis to balance the endosmosis, and this then in the roots resulted in excretion of injurious materials. There had arisen at this time also a suggestion that toxic root excretions or the decayed remains of plants poison the soil for the plants producing them. While no experimental data were available the observations on crops had made this soil toxin hypothesis seem probable.

Schleiden's theory of the organization of the embryo from the tip of the pollen tube had just been displaced by the careful studies of Amici and Hoffmeister demonstrating the presence of the egg-cell in the embryo sac and the fertilizing action of the pollen tube. Sperms had been seen in the Cryptogams, and the essential features of the fertilizing process had been well described by several investigators.

Geotropism was on the verge of being discovered, for Knight's work had already been published, demonstrating reaction to centrifugal force, yet as late as Schleiden's 'Principles' it is stated that, "We know nothing at all respecting the cause of the direction taken by the germinating plant" and the action of gravitation as a stimulus was not accepted. The directional action of light on the stem was recognized, and the "sleep" reaction of many leaves was a well-known phenomenon. However, Sir Humphrey Davy, in his 'Elements of Agricultural Chemistry,' as late as 1813, had denied the concept of irritability in plants.

Controversies at this period were numerous, due to preconceived notions, inaccurate observations, and misinterpretations. While in the main Schleiden was a progressive scientist, there were several problems in which, because he took the cautious,

conservative attitude, he failed to espouse the new and correct ideas. While his criticisms of his predecessors are often severe and he often places little reliance on their work, this attitude seems to be due largely to his keen appreciation of the necessity of controlled experiments and of accurate and frequently repeated observations. One other source of his strictures was his repudiation of the popular method of almost complete dependence upon analogies between plants and animals. Although his extreme attitude was finally to be overthrown yet no doubt he was correct in believing at that time that these analogies were too easily accepted without adequate scientific evidence.

It is clear then that at the beginning of Sachs's activity the general outlines of our new plant physiology had been developed, but many of the major concepts were still seriously questioned while many important details and some major fields needed careful experimental study. Moreover, the separation of this field of investigation from that of general botanical studies had not taken place.

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THE CONTRIBUTIONS TO BOTANY OF JULIUS VON SACHS[1]

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Director Moore has very wisely divided the programme into three epochs,—Plant Physiology as Sachs Found It, The Contributions of Sachs to Plant Physiology, and Progress in Plant Physiology since Sachs. By this plan an opportunity is given the several speakers of presenting to their listeners a true perspective of the field under consideration, and of the position and influence therein of Sachs, its central figure. The first epoch we have had already passed before us, and I feel certain all have been impressed with the slow advance of physiology and of botany until approximately the middle of the nineteenth century, when, with new methods and directive thought so essential to real progress, a new era was ushered in. In this era Julius von Sachs was to play a most important rôle.

In presenting the contributions which Sachs has made, I feel that full justice cannot be done him should I confine my remarks strictly to physiology. One of his most far-reaching and lasting contributions was the masterly manner in which he coördinated the several fields of botany, and made the *functional* plant the unit of interest. This he did in his 'Lehrbuch,' first edition, 1868.

The status of botany, particularly in America and England, at that period was deplorable. The few bold spirits that ventured into the botanic field were compelled to make their way to Germany to sit as disciples at the feet of the great masters,—De Bary, Sachs, Strasburger, etc., successors or contemporaries of Schleiden, von Mohl and Hofmeister. To this galaxy of investigators, largely in the period from 1840 to 1880, we owe the most distinctive discoveries and advances in the history of botany, and to the genius of Sachs, the organization of these into a new and virile botany. When I seem to digress from the more limited subject assigned me and speak of the contributions that Sachs

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made to the field of botany as a whole, I do so to emphasize the part the physiology under his leadership has played in it, and the masterful manner in which he welded the heterogeneous fragments of independent research into a real science of botany with all its branches definitely interrelated. In other words, he gave us for the first time a text-book in which the plant as a *functional machine* is lucidly and accurately brought before the student. Furthermore, to him, more than to any other contributor to the field of botany, do we owe the deep significance of the physiological division of labor in the interpretation of anatomic and morphologic structure.

For a proper appreciation of the conditions then (1868) prevailing in the field of botany, and the influence of Sachs in the molding of future progress, I cannot do better than to have former students of Sachs, men with whom a number of us have or had personal acquaintance, speak to us with their accustomed accuracy and freshness.

Farlow, in his presidential address before the Botanical Society, Cleveland, 1913, says:

> "In the laboratory [De Bary's], I noticed that the students seemed to refer frequently to a book of which I had never seen a copy or even heard. The book was Sachs's 'Lehrbuch,' second edition, 1870. I bought the book and was perfectly amazed. I had never dreamed that botany covered so large a field. The 'Lehrbuch' was an admirable summary of what was known of all departments of botany up to that date, well written and excellently illustrated. The fourth edition, which appeared while I was in Strassburg, was still better. On looking at the second edition a number of years later, I noticed what seemed to be a curious omission. No mention whatever was made of bacteria. In the fourth edition they are mentioned under *Schizomycetes*. The absence of reference to bacteria in the earlier edition, however, was not an omission. There were no bacteria until Cohn published his 'Untersuchungen über Bacterien' in 1872. The fact that forty years ago Sachs had never heard of bacteria, while to-day life has almost become a burden, one hears so much about them, is a striking instance of the rapidity of development of a subject having a practical as well as a theoretical value. I know no single book which has had so great an influence in shaping the course of modern botany as Sachs's 'Lehrbuch.' It may be that the facts there given were generally known in Germany, but they were not known in other countries. On returning home by way of England in 1874, I showed my copy of Sachs to several English botanists and it was evident that it was quite new to them. It was certainly unknown in America. If imitation is the sincerest flattery, the value of Sachs's 'Lehrbuch' was quickly recognized, for, using it as a model or basis, there soon appeared a large number of really excellent textbooks in various languages in which one recognized Sachs translated, Sachs con-

densed, Sachs diluted, Sachs trimmed to suit local demands. Publishers, were they capable of gratitude, would have erected a monument to Sachs's memory long ago. Draughtsmen, on the other hand, had little reason to bless his memory. Even now we can hardly open a new text-book without seeing the inevitable 'after Sachs.' "

From this brief extract you will note the status of botany in America in 1870. Let us next turn to England and hear in turn from Vines, Scott, and Bower an expression of the condition of botany in that country in the middle of the decade, and an appreciation of Sachs as lecturer and teacher, and of his great influence in molding and directing a new and lasting trend in botanic teaching and investigation,—a trend that has gained in impetus with a younger and better-trained generation all too frequently innocently ignorant, I am sorry to say, of a debt it owes to him to whom we this day in gratitude pay homage and tribute.

Quoting from Vines:

"In 1876 I had been appointed an Assistant Tutor at Christ's College, Cambridge, for the benefit of the increasing number of the undergraduates who were reading Natural Science, and had begun to lecture there on Botany, though I had no means for carrying on any practical work. . .

"It seemed to me, therefore, essential to equip myself further for future work by spending what time I could spare in some well-known laboratory. As such equipment was quite unobtainable in Britain, my thoughts turned naturally to Germany. Then arose the question of to which laboratory I should visit. At that time the best known of the German botanists, other than systematists, was Hofmeister, though his doctrine of 'alternation of generations' was still regarded with some suspicion by those of the more orthodox British botanists who knew anything about it; had he been still at work, I should probably have gone to him at Tübingen, but he had quite recently died. Considering that the greater part of my botanical lore had been derived from his immortal *Lehrbuch* (3rd ed. 1874), I had no hesitation in deciding that I must go to Julius Sachs at Würzburg, who was then at the zenith of his activity and fame, and whose laboratory was renowned for its physiological work. Having obtained leave of absence for the Easter Term from the College authorities, and armed with an introduction from Mr. Thiselton-Dyer, I accordingly set out for Würzburg in March, 1877. . .

"On beginning work in the laboratory, I found myself to be the only advanced student, so that I had the great advantage of the undivided attention of the Professor, which I gratefully acknowledge was ungrudgingly bestowed. The special subject of study suggested to me was that of growth, especially in its relation to light, and Sachs placed at my disposal and demonstrated to me all the available apparatus for measurement. Such was my first introduction to practical plant-physiology.

"Naturally I saw a good deal of the Professor in those early days, and an acquaintanceship developed into an intimacy which continued unbroken until his death in 1897. I often accompanied him for a stroll round the Botanic Garden

or in the shady avenues of the town, when he won my admiration by his remarkable conversational gift, discoursing of many things, not always botanical by any means, but ranging widely to include such topics as the philosophy of Herbert Spencer or the works of Lecky. . .

"He was then engaged upon his experiments, by the lithium-method, on the rate of the transpiration-current, in which I occasionally helped him and had the opportunity of observing the precision and skill with which he devised and carried them out. . .

* * * * * * * * *

"Accordingly I returned to Würzburg in April, and found the laboratory much as I had left it three years before. But the 'Assistant' was now Dr. Goebel (in after years Professor of Botany at Munich). . .

"Professor Sachs was as friendly and energetic as ever, though I did not see so much of him as in 1877, for he was engaged not so much in experimental work as in the preparation of his remarkable papers on 'Stoff und Form der Pflanzenorgane.'

"I did not, on this occasion, undertake any definite piece of work, but continued the investigation of the chemical composition of aleurone on which I had been engaged off and on for some time, in which the Professor took a lively interest as it was a subject to which he had not devoted much attention. . .

"But the outstanding feature of the Semester was the Professor's course of demonstration-lectures on plant-physiology. The lectures were given on Saturday mornings, and each lasted for about two hours. Here Sachs was at his very best, inspired by enthusiasm for his subject which he did not fail to communicate to his audience. The eloquent speech; the pictorial illustration, generally by means of large sheets of white paper and a stick of charcoal instead of black-board and chalk; the manipulative dexterity; all these combined to rivet attention. . .

"Such is my story, but it would be incomplete were I to conclude without some moral reflections. The first and most obvious is—how simple, we should now call them inadequate, were the means with which the great advances in botanical science, between 1840 and 1880, were achieved in Germany! Clearly great epoch-making discoveries do not depend upon huge superlatively equipped laboratories; it is the man, not the mechanism, that counts. The next takes the form of the question—was it worth while to go to Germany to study? My answer is a strong affirmative. Brief and fragmentary as were my studies there, I recognise how great was their advantage to me, and I do not forget the debt of gratitude that I owe to the Professors who so kindly received and helped me. If the enquiry be pressed further—what was it that I gained? my answer is that I gained, not so much actual knowledge as what, for lack of a better term, I must call inspiration, the right point of view; in fact, a sort of botanical 'confirmation' at the hands of the pontiffs of the science. To make my meaning clear, I may explain that though I had read much of what there was to read on plant physiology (it was relatively little in 1877!), I had had no opportunity of comparing notes with another plant-physiologist until I went to Sachs, the fountain-head of so much of the knowledge which I had laboriously gleaned from books. His expositions of his own work, and his criticisms on the works of others, including my own, were a liberal education. I sought and found in Germany what was unobtainable in my own country."

Ten years following the experiences related by Farlow we find Scott (1880–82), upon the advice and support of Thiselton-Dyer and Vines, a student in the laboratory at Würzburg. He tells us:

"At that time, Sachs had a high reputation in England, owing, in a great degree, to his famous Text-book, of which an English edition, translated by Bennett and Thiselton-Dyer, had already appeared in 1875. This had a marked influence on the progress of Botany in England. . .

"Sachs was the best lecturer I ever heard. Hard work at German, before starting from England, had prepared me to understand what I heard without much effort. The lectures were extraordinarily clear, interesting, and sometimes amusing. . .

"The brilliancy of Sachs's lectures was enhanced by the beauty of the sketches which he made to illustrate them. Usually these were on the blackboard, but when any specially elaborate structure was to be shown, a sheet of cartridge-paper was brought in, and Sachs made, before our eyes, a finished chalk drawing in colours—truly a wonderful performance. Later in the season Sachs started his physiology lectures, given on Saturdays. In this case, as experiments had to be demonstrated, two hours (actually one and three quarters) were allowed. Though I was never attracted to physiology, it was a great experience to witness these expositions by the greatest plant-physiologist of his time. . .

"Late in July, as the result of a conference with Sachs and Goebel, I decided to work for the Ph.D. At that time the subject proposed for my dissertation was the relation between leaf and branch. . .

"On returning to Würzburg after the long vacation, I found that Sachs had changed his mind; he no longer thought the morphological subject suitable. Such questions, he said, were not so much thought of in England as in Germany. I had never taken much to the plan myself, and was relieved when Sachs advised me to transfer my energies to a purely anatomical investigation—the development of articulated laticiferous vessels. This eventually formed the subject of my dissertation.

"At that time the development of laticiferous tubes in general was not so well understood as it is now; in particular, the origin of the articulated type by cell-fusion was not finally established. This was the problem which I was to help in solving."

We have heard from Farlow, a student of cryptogamic botany; from Vines, a student of plant physiology; from Scott, a student of paleobotany; and, finally, we shall hear from Bower, a student of morphologic botany, whose noteworthy contributions in that field no doubt have been influenced by his contact with Sachs. Bower says:

"Within a few years of Hofmeister's 'Vergleichende Untersuchungen' (1851) came the 'Origin of Species' (1859). It then appeared as though a theory of evolution had merely to adopt the results already demonstrated by him. After events so stirring we need not be surprised that a pause should follow. It took time for men to realise the bearings of the new views, and still more to convert them into action. Botanically little change appeared immediately in Britain;

but within a decade an event happened in Germany which was to produce far-reaching results. It was the publication of the *Text-book* by Sachs.

"That work was written with consummate judgment, and illustrated with all the skill of a trained draftsman, who was also a keen observer. Sachs was, I believe, the son of a wood-cut artist, and had been himself trained as such. But beyond his keen vision and artistic touch, he possessed also a philosophical outlook combined with keen receptivity. These faculties made him the best possible exponent of the results of those, such as Hofmeister, whose powers of exposition were less than his own. Little wonder that the *Text-book*, which embodied not only their results but also a vast extent of Sachs' own observations, morphological and physiological, had a phenomenal success. The first English edition published in 1875 was based upon the third and fourth German editions, and it fell into my hands at once on its appearance. It came as a revelation to the group of enthusiasts beginning to gather round Vines at Cambridge, and supplied the text upon which much of our work was based. We felt then that we were daily seeing things not, it was true, new to science, but at least observed for the first time in Britain. Some of us, however, naturally looked further to the living source; and when Vines went to Würzburg in 1877, though still an undergraduate I joined him for some weeks in the summer, to sit at the feet of Sachs himself. .

"Looking back upon this period of preparation, there is no doubt that it was necessary at the time that some of us should become personally acquainted with German laboratories and methods. Going to foreign schools was the readiest way of making up that backwardness which had resulted from the academic apathy of a generation of the teaching botanists of Britain, and from their failure to keep pace with those advances in observation and laboratory technique which had grown up on the continent. . .

"It is for those who direct the progress of the teaching of the science to take care that they shall not, by allowing too early specialisation along applied channels, send out specialists too quickly and imperfectly qualified. But the more grave risk is that they should allow the central institutions to lose again their hold upon the broad stream of pure science, as their predecessors did at the middle of the last century, by over-concentration upon special requirements."

From the extracts that I have read, it is very evident that the contributions of Schleiden, von Mohl, Hofmeister, De Bary, Naegeli, Sachs, and others, made during the middle decades (1840–1880) of the nineteenth century, and which marks that period the most notable in the history of botany, had little affected the trend of botany in America or England. It was the publication of Sachs' 'Lehrbuch' in 1868, and especially the translation of a later edition into English, that proved the most potent factor in the development of botany in English-speaking countries.

The 'Lehrbuch' owed its unprecedented popularity and success to: (1) the fact that in it for the first time the widely scattered and, in many instances uncorrelated, discoveries of Sachs' predecessors and contemporaries were skillfully coördinated with his own, and

presented in a lucid, attractive style, and illustrated with figures that to this day are unsurpassed; to (2) the plan well-nigh faultless in conception and execution, in which the well-balanced treatment of the subject matter is interwoven with theories, critique, suggestive problems, and prospective lines of research; and finally, to (3) the revolutionary, I am tempted to say, treatment by which the whole of botany from cell through tissues, taxonomy, morphology, anatomy, ontogeny, and phylogeny, and the origin of species through the Doctrine of Descent, receive thoughtful consideration and masterful coördination. Throughout the book one is impressed with the persistence with which a single motive, namely, *function*, pervades and dominates the whole, and reveals to the thoughtful reader the inner workings of a great mind. In fact that seemed to have been his aim and endeavor, for we read in the preface of his Lectures as follows,—"It is not only the right but also the duty of anyone who lectures, however, to place in the foreground his own mode of viewing the matter; the audience wish to know and should know how the science as a whole shaped itself in the mind of the lecturer, and it's comparatively unimportant whether others think the same or otherwise."

Sachs, by placing emphasis on the significance of response, brought to the front the importance of the *protoplasm* of the cell as the responsive material possessed with innate developmental and adaptive potencies, and this point of view was in no small measure responsible for the change in the method and outlook of anatomy, morphology, and taxonomy. It is from this conception only, he maintained, that the origin and persistence of the great groups of the Plant Kingdom can be explained. In like manner it was the environment acting on the responsive protoplasm that brought on physiological division of labor, and with it, differentiation. This was in direct conflict with the phylogenetic view held by the morphologists and anatomists of his time, and, despite the strong criticisms of De Bary in his attempt to uphold the classification of tissues based on the history of development, the physiologic classification into epidermal, fibrovascular, and fundamental, all derived from meristem, prevailed.

Perhaps his deepest philosophic efforts were concentrated on

the finding of an hypothesis that should be helpful in the elucidation of differentiation and organ formation, and the effects of the environment on the same. In a series of contributions on 'Stoff und Form der Pflanzenorgane,' Sachs calls our attention to the impossibility of a formal morphology such as then prevailed, interpreting the significance of organs in any other manner than "als für sich Existirendes, unabhängig von jeder materiellen Grundlage angesehn." In his attempt to formulate a causal relationship between the development of an organ and its function, which he found impossible experimentally to demonstrate, he gave to us an hypothesis, which Loeb, writing in 1906, states is the "only scientific hypothesis of morphogenesis which we thus far possess." In this hypothesis, Sachs maintains that the only adequate explanation for the formation of new organs, of flowers, or of the regenerative processes must be sought in plastic materials, as yet unknown, and produced in the living protoplasm. These "formative stuffs" present in extreme small quantity, on reaching an organ, direct its growth and development in a specific manner. I need not proceed further along this line for I believe it perfectly evident that our modern conceptions of "growth-promoting," "growth-inhibiting," auxamones, yes, even hormones, are rooted in this hypothesis.

In like manner the developmental process proceeding from the egg finds here its only explanation. It is interesting to note the parallelism of expression used by Wilson in the last edition of his 'The Cell in Development and Heredity,' and by Sachs more than fifty years previously. Wilson says:

> "That a single cell can carry the total heritage of the complex adult, that it can in the course of a few days or weeks give rise to a mollusc or a man, is one of the marvels of nature. In attempting to attack the problems here involved we must from the outset hold fast to the fact that the specific formative energy of the germ is not impressed upon it from without, but is somehow determined by an internal organization, inherent in the egg and handed on intact from one generation to another by cell-division. Precisely what this organization is we do not know. We do know that it is a heritage from the past somehow perpetuated by cell-division, and that development is only a further extension of processes that have been going on since life began."

I follow, quoting from Sachs:

> "So wenig wie die ungeschlechtliche Fortpflanzung ist auch die sexuelle dazu berufen, im strengsten Sinn des Wortes einen neuen Organismus zu produziren;

die Elemente, aus denen dieser entsteht, sind selbst nur Produkte der embryonalen Substanz einer früheren Pflanze und schliesslich können wir sagen: *das was sich seit dem Beginn des organischen Lebens auf der Erde kontinuirlich immerfort in dem ewigen Wechsel aller Gestaltungen, in dem beständigen Wechsel von Leben und Tod lebendig erhalten und sich immerfort regenerirt hat, das ist die embryonale Substanz der Vegetationspunkte, die in bestimmten Fällen sich in männliche und weibliche differenzirt, um sich dann wieder zu vereinigen.* In diesen winzig kleinen Stoffmassen hat sich das organische Leben in dem langwierigen Verlauf der geologischen Epochen beständig selbst erhalten; diejenigen Thiele der Pflanzen, welche sich dem Auge unmittelbar darbieten, die ausgewachsenen Wurzeln, Sprossachsen, Blätter, die Holzmassen u. s. w., dies alles sind Produkte jener embryonalen Substanz, die sich beständig regenerirt, während diese ihre Produkte zwar an Masse millionenfach sie überwiegen, aber keiner Regeneration fähig sind; sie sind es nicht, in denen sich die Kontinuität des organischen Lebens erhält, aber sie sind es, die durch ihre gemeinsame Arbeit den Assimilationsprozess und den Stoffwechsel hervorrufen und ein sehr kleines Quantum der Substanz, die sie zu ihrem Wachsthum nicht selbst verbrauchen, wird zur Ernährung der embryonalen Substanz der Vegetationspunkte und Sexualzellen benutzt."

The two quotations taken from authorities separated by two generations in time show how well Sachs had conceived and developed these problems so fresh and fundamental to biologic thought of to-day.

Further, it is of interest to note that in the above quotation we find the idea of the continuity of the embryonic substance beautifully and unmistakably expressed three years before Weismann gave to us 'Die Kontinuität des Keimplasmas,' destined to exert such a tremendous influence on the biology of the latter part of the nineteenth century.

Continuing along the line of his studies on embryonic tissue, we find in his 'Ueber Wachsthumsperioden und Bildungsreize' a mass of material worthy of the deepest reflection by present-day physiologists. Time and space permit me to cite only two paragraphs, which, however, seem to me to express the key-note to effective physiologic experimentation with plants:

"Durch den in den Pflanze thätigen Gestaltungstrieb wird jedes sich entwickelnde und wachsende Organ, selbst jeder Theil eines solchen, in seiner äusseren Form und seiner inneren Struktur fortschreitend verändert: das Organ ist heute nicht mehr dasselbe Ding wie gestern und wird morgen wieder ein Ding mit anderen Eigenschaften sein, selbst wenn man dies an der äusseren Form und der mikroskopischen Struktur nicht wahrnimmt.

"Wird nun das sich entwickelnde, wachsende Organ von äusseren Einwirkungen betroffen, welche die Art seines Wachsthums verändern, so muss diese Reaction verschieden ausfallen, je nachdem die gleiche äussere Einwirkung das wachsende Organ gestern, heute oder morgen trifft."

I feel confident that the discordant results with the use of similar organisms now so frequently reported may be greatly lessened through a more conscientious study of the principles suggested in the above quotation. The physiological phase of development at the time of experimentation, and a more detailed attention to the environmental factors to which the plant is exposed preceding the experiment, should receive the same serious attention now as then.

Proceeding from these philosophic aspects of the meristem or growing tip, I may pass to a brief consideration of his views on cell activity and cell relation. Because of his strong bias, and consistent with his view concerning the developmental process, Sachs took the position very effectively described by Hertwig as follows:

> "Although from the point of view of the morphologist it has become more and more imperative to regard the cell as the unit of the higher organism, still, from the physiological point of view, the higher organisms must be regarded as masses of material of structural parts subordinate in function to the whole, and displaying only a limited division of capacities. And so the cell theory, according to which the cell was exalted unduly as the unit of life, the center of life, the elementary organism, must take limitation and correction from these wider views."

With the emphasis placed on the organism rather than on the cell, Sachs clearly saw that the complex of tissue cells in the plant, encased as they are in cellulose walls, must have some provision by which the whole is organized into an interacting community and suspected protoplasmic connections long before their actual demonstration. In a series of articles under the general head 'Beziehungungen zwischen Zellbildung und Wachsthum,' he makes clear his ideas on the relation between growth and cell-division, and insists that growth is primary and cell-division secondary. Here he also develops his principles of cell-division as (1) cells divide into equal parts, and (2) each new plane of division intersects at right angles the previous one, subsequently elaborated by Hertwig. His elaborate studies on the geometrical relations of cleavage-planes in growing plant tissues which are either anticlinal or periclinal, received much attention and are not without interest to-day. He was the first to call our attention to the relation between size of cell and size of organism.

I shall next pass to the consideration of the more important

contributions in experimental physiology contributed by Sachs, and on which the superstructure of present-day physiology was built. The task of presenting the gist of one hundred papers is not an easy one, and time does not permit of great detail. I shall therefore confine myself to brief remarks concerning those researches that, in my opinion, were most important in the development of experimental physiology of which he is the recognized founder, and as my guide I shall, in general, follow the headings as given in his 'Gesammelte Abhandlungen.'

In the first section, "Ueber Wärmewirkungen an Pflanzen," we find several contributions of present-day interest. His studies on crystal formation in the freezing of plant tissue corrected false conclusions that had been previously held, but he was unfortunate in his explanation of the cause of death. His studies on "Vorübergehende Starre-Zustände" (1863) furnished us new and detailed information regarding heat and cold rigor, and gave us the terms phototonus and thermotonus. Here as elsewhere in his discussions on response he says that "irritability both in the vegetable and animal kingdom must in the main be full of purpose." The use of the word purpose has misled many botanists. They not infrequently have accused him of having marked teleological views. This, I believe to be wrong, and a careful reading of his contributions will, I think, correct such an impression. A single quotation from Sachs will make this clear:—"But the fact that, formerly, purpose in the mechanism of organisms was referred to causes other than now, is no reason for robbing our language of a pregnant term. By the expression, This or That mechanism has a purpose in an organism, one understands really nothing more than that this contributes to the ability of the organism to exist." In his studies on germination as affected by temperature, and of maximal temperatures on vegetation, he presents a wealth of information obtained by experimental methods which was new and stimulating then, and to which we even now return. In these papers the terms minimum, optimum, and maximum as the cardinal points were for the first time employed, and the effects of supra temperatures on the several cell functions, for example, turgor and permeability, permanently established. Mention should also be made here of the effects of

minimal temperatures required for chlorophyll formation, even in the gymnosperms where ordinarily chlorophyll forms in the dark.

The second section, "Ueber Licht-Wirkungen an Pflanzen," deals with the transmission of light through plant structures, and brings into use the diaphanoscope revealing the change in the transmitted light due to chlorophyll absorption; with the morphogenic influence of light on the growth, unfolding, etc., of the several plant organs; with the action of colored lights on plants in which his chief object was to determine experimentally the similarity or dissimilarity between the action of different lights on the chlorophyll formation and gas evolution in plants and on silver chloride. In the same paper he investigated chlorophyll formation and tropic response in blue and orange light,—double-walled bell jars—and the disintegrating action of this light on a chlorophyll solution.

The third section, "Ueber Chlorophyll und Assimilation," brings to us a series of papers generally conceded as among the most stimulating contributions to physiology. Here he demonstrates that starch is the first distinctly recognizable product in photosynthesis, and related its formation to the action of light on chlorophyll. Further, he enters into a quantitative study of the product, gravimetrically and with the still much-used iodine test. With the use of tin-foil partially covering the illuminated leaf, he shows the dependence of the product on light, and that it is strictly localized; he shows its decrease under less intensive insolation, its disappearance in the dark, and surmises that it is converted into sugar for translocation.

The fourth section, "Ueber Bewegungen des Wassers in Pflanzen," considers among other things, the experimental evidence on which he based his imbibitional theory. Unfortunately the theory itself has been found wanting, though it must be admitted that many of the details that Sachs gave to us are used in the newer and more satisfactory theories of to-day. To our knowledge of transpiration he added a great deal, and started lines of investigation which are at present still receiving well-deserved attention. His experiments on the saturation capacities of soils of different chemical and physical composition, and the amount of water that a

root system is capable of absorbing, were fundamental in their conception and still offer problems in modern physiology. He successfully correlated transpiration with soil moisture, temperature, acid and alkaline reaction, etc., and insisted that it must be considered with other vital processes of the plant. He recognized the difference between cuticular and stomatal transpiration, and attributed the much greater quantity of the latter to the intercellular spaces in the mesophyll with which the stomates communicate. He supplemented the views of Schwendener and suggested that the turgor phenomena are traceable to the osmotically active substances produced by the chloroplastids in the guard cells, and made the stomates the path of gaseous interchange. He held untenable the view that root-pressure is a factor in the movement of water, but attributed to the suction force of transpiration very much the same office as do the accepted theories of to-day.

In the fifth section, "Ueber das Verhalten der Baustoffe bei dem Wachsthum der Pflanzenorgane," he follows the transformation of the oil in oily seeds into starch and stated that in all probability it was translocated as a sugar. In a series of beautiful figures and comprehensive tables he indicates the presence or absence of oil, starch, or albumin, and thus strengthens his physiologic interpretation of the tissue systems. Following this are four contributions on the germination of the bean, grasses, date, and onion, all worked out with the same care and laying the foundation for all subsequent studies. The last paper in the series concerns itself with the "acid, alkaline, or neutral reaction of living cell saps,"—a title that sounds extremely modern.

The sixth section, "Ueber das Wachsthum von Sprossen und Wurzeln," brings to us his epoch-making studies on growth in which temperature and light are considered in their influence on daily periodicity in growth. Here, too, are given us the observations that brought to our attention for the first time that distribution in the growth phase that he named the Grand Period of Growth; here he gave to us the auxanometer; described and defined nutation in contrast to circumnutation; showed the effect of the environment—air, water, or soil—on the growth of main and lateral roots and of the angle of the latter to the main root, and the distribution of growth in the responsive processes to

gravity, etc. Through his simple demonstration of the growth of a root into mercury, he silenced the contention generally held that the curvature is a mechanical process due to the action of gravity on the root mass, and added another convincing point to his contention that all responses are vital.

In the seventh section, "Ueber die Tropismen als Reiz wirkungen," we find him developing his vital theory to irritability. Here we have the first and most conclusive evidence ever offered of the effect of age or physiologic phase, and of the effects of previous exposure, on the reaction of the plant organ. He calls to our attention the difference in response to the same stimulus of the main and the lateral roots, and introduces the terms orthotropism and plagiotropism. He demonstrates the response of the root to differences in moisture, hydrotropism, and gives us his simple but effective sieve method. In the response of plant organs to light, he lays stress on the importance of the direction of the rays, invents and illustrates the use of the klinostat in investigations of this sort. He calls attention to the difference between growth response and turgor response as illustrated in pulvini.

I feel that I must not close this paper without some reference to the cordial interest that Sachs at all times maintained toward the young men in his laboratory, and his deep conviction that the teaching process is one worthy of serious attention and concern. The following story told me by Professor Fritz Noll only a year after Sachs' death, I am sure, will be of interest to all: Noll had been appointed assistant to Sachs and was entering with fear and trepidation the lecture room for his first lecture. He was met by Sachs who told him that he would find the door leading from his study into the lecture room slightly ajar. This, he said, was not with an eaves-dropping intent, but rather for the purpose of following his lecture while at work, thus to be able to give suggestions for possible improvement. He further requested that Noll call at his (Sachs') office immediately following the lecture. I am sure that all of you can imagine the strain on a young assistant when the master listens intently to the efforts of the amateur. Noll told me that the training there received was of the very best. Always kind and considerate, Sachs would commend Noll on the

manner of presentation of one phase of the subject, but would show him, with kindly consideration to his feelings, how the presentation of another phase could have been much improved.

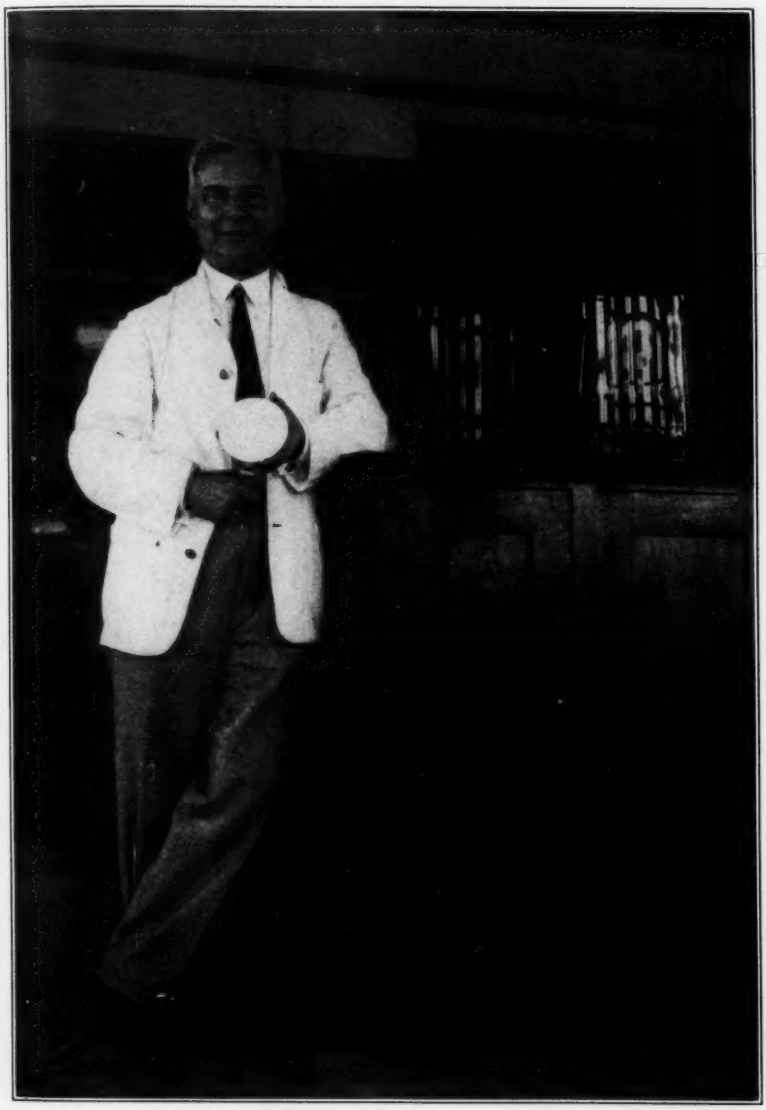
Thus I have briefly reviewed the more important contributions to botany in general, and plant physiology in particular, made by Sachs, the one-hundredth anniversary of whose birth we are here met to celebrate. The number would be greatly increased had I included the many and noteworthy contributions made in his laboratory by such students as Goebel, De Vries, Pfeffer, Vines, Bower, etc. Truly, I think, can the criterion which he used in measuring worthiness for consideration in his History of Botany, be applied to him,—"I have, therefore, singled out those men as the true heroes of our story who not only established new facts, but gave birth to fruitful thoughts and made a speculative use of empirical material."

Explanation of Plate

PLATE 2

Two of three original Bell jars for light experiments made for and used by Sachs at Bonn. Prof. Max Koernicke holding a round marble plate, original root-etching experiment.

Photo by Prof. F. E. Lloyd.



HOTTES—SACHS'S CONTRIBUTIONS TO BOTANY

A HALF CENTURY OF PLANT PHYSIOLOGY[1]

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As has been clearly shown by the preceding essays important work had been done in the mechanics of plant life two centuries before the time of Sachs. He was therefore not the founder of the subject. His activities, however, have exerted a more profound influence on the study of life in plants than those of any worker in the subject and started physiology on a wholly unpredictable development.

The character of laboratory texts, lectures, instruction and research in the dynamics of plant life for the last half century was determined by the experimental investigations and theoretical conceptions developed by Sachs and the group of able workers who participated in the activities of his laboratories. When it is recalled that the list included Baranetzky, Bower, Brefeld, Francis Darwin, Detlefsen, Elfving, W. Gardiner, Godlewski, Goebel, Hansen, Hauptfleisch, Gregor Kraus, Klebs, J. Loeb, Millardet, H. Müller-Thurgau, Moll, Noll, Pedersen, Pfeffer, Prantl, Reinke, D. H. Scott, Stahl, Vines, deVries, Marshall-Ward, Weber, Wortmann, and Zimmermann, nothing more need be said as to his dominating influence on the development of the subject.

Naturally these men, as leading figures in the last decades of the century and the beginning of this, continued work begun with his advice and direction. The literature of the eighties and nineties shows that repetitious tests of the earlier results with extensions and refinements in experimental procedure absorbed a large share of the energies of workers in the laboratories of Central Europe, Great Britain, and America during this period. Work on sensitive tendrils, tropisms, and curvatures, and etiolation, may be cited as illustrations.

Sprouting, germination, and growth in its widest sense came in for great attention, especially since these activities were

[1] A paper read at the celebration held at the Missouri Botanical Garden, December 27, 1931, in honor of the one-hundredth anniversary of the birth of Julius Sachs.

made the criteria of so many tests of nutritive or environic factors. The conception evolved by Sachs of a specific formative material necessary to growth ran its course of usefulness until supplanted by modern studies of accessory substances and regeneration. That many of the findings of Sachs were modified or reversed by the results of more detailed experiments and with improved apparatus and advanced knowledge in no wise detracts from the enduring value of his achievements.

The most valuable feature of the Sachsian contributions was that they set up no falsely appearing dead ends. Down a hundred corridors one might sense doors opening to new vistas. Immediately after Sachs the mechanics of cell-action and the visible features of structure and architecture of protoplasm were followed to the limit of microscopic vision. It soon became evident that the nature of protoplasm was not to be apprehended on the basis of spongy, emulsoid, or foamy structures revealed by the direct-vision microscope. Nearer approach to the essential and characteristic features of living matter was to be made only by studies in the realm of the ultra-microscopic, in which the theoretical conceptions of the colloidal physicist were relied upon to furnish a picture of the molecular meshwork.

The realization of the polyphasic nature of protoplasm has prepared us for the acceptance of the conclusion that the ultramicroscopic and filter-passing viruses are in fact ultimate centers of transformations of energy ordinarily attributed to living things.

Protoplasm was earlier supposed to consist of a mixture of proteins, but biochemical researches have made clear the presence of lipoids in the plasmatic mass and their importance as a colloidal component as well as the part they may play in energy-transformations.

Microdissection has now begun to play an important part in the study of essential characters of chromosomes and other bodies as well as of the plasmatic mass. The earlier conception of the cell-wall as a stratified cellulose formation has been gradually modified until at the present time it is realized that its constitution is determined by the protoplast with which it is intimately and actively connected, so that the expression non-living wall may not be correctly applied to any cell with surviving plasmatic material.

If it became necessary, however, to designate the single conception which has played the greatest part in the development of physiology in the last half century, the choice would undoubtedly be that of electrolytic dissociation and its concomitants. While the actual origin of this conception cannot be given, its formulation in a manner making it available to the physiologist was by Arrhenius in the eighties. With Pfeffer's results in osmosis and DeVries' determinations of isotonic coefficients it constitutes the basis of modern plant dynamics.

The ion or charged particle is now the unit to be considered whether mobilities, interferences, and antagonisms of elements are to be studied in turgidity, permeability, and in nutrition, or whether the electro-kinetic potential of the molecular meshwork of protoplasm is being considered in the connection with hydration and growth.

This paper would be extended far beyond its desirable limits in any attempt to describe the modifications of ideas of plant nutrition in experimentation and in agriculture which have resulted from studies in this field.

Perhaps the earliest effectual co-operation of chemists in the physiological field was that which came in the study of the enzymes. Some of these substances were known in the time of Sachs. Later contributions have consisted in finding a large number of these organic catalysts and in delimiting their specific action, as well as the range of their activity with respect to concentration of the medium, the accumulation of their products, and their relations to temperature. The proteinaceous character of the enzymes has led some writers to consider them as living matter. Some enzymes are known to carry a mineral element in their molecular mesh-work. It is to be recalled here that in addition to these complex bodies simpler catalysts such as some of the mineral elements have become known.

The study of the effects of radiant energy has been extended to observations of great delicacy in phototropism. It is a singular fact that when the philosophic definition of consciousness that makes this state depend upon modification of one irrito-motile reaction by another is applied to plants we do have activities that are, academically speaking, conscious. I refer particularly

to the case where an upright flower stalk in its development reaches a stage where it changes its position from the erect to the horizontal in response to gravity: it does so by a curvature in a direction determined by the impinging light.

Outside of this the basic unity of living matter yields no support for Aristotle's notion of an ascending complexity of living matter from the simplest plants to man. Plants and animals represent the two main surviving streams of living things in which only the inseparable colloidal characters of their living matter are the basis of comparison.

The fact that the organisms are so widely apart in their forms and modes of living calls for dissimilar perceptive mechanisms and transmission of stimuli. The wholly mystic nervous mechanisms and pulsations of Bose have so far eluded all observation, and nothing in the implied conceptions may be properly included within the domain of science, or of reality, or may be deemed worthy of metaphysical consideration.

It is of interest to recall that Sachs, commenting on the futility of the type of explanation in question, said: "We have no necessity to refer to the physiology of nerves in order to obtain greater clearness as to the phenomena of irritability in plants; it will perhaps, on the contrary, eventually result that we shall obtain from the process of irritability in plants data for the explanation of the physiology of nerves, and this, although it is yet a distant hope, gives a special attraction to the study of the irritable phenomena of plants."

Progress in the elucidation of the physical processes of transmission of nervous impulses in animals has, however, gone much farther than our understanding of homologous phenomena in plants. There is much sound evidence of effects being carried some distance by discrete particles or hormones, while in other cases the view that impulses may consist in disturbances of the electro-kinetic balance is favored. The study of the effects of interrupted action of stimulatory, regulatory, excitatory agents on "sensitive" organs has yielded some results which take on added value when compared with reactions in animals.

The study of the effects of duration, intensity, as well as wavelength, in photosynthesis is yielding some valuable results, while

the direct action of radiation in the region of the ultra violet and beyond on living matter is now known to be a matter of great importance in heredity as well as in growth and development.

The most prominent of the basic conceptions of plant physiology which have become the foundation of separate branches of science was that embodied in de Vries' mutation theory of evolutionary procedure. That differentiations in a line of descent should be by measurable units is a theoretical conception essentially physiological, matured in the mind of de Vries who had already contributed studies of electrolytic dissociation and its physiological implications.

It may be recalled that the evolutionary point of view received its earlier support from experimental evidence obtained by Charles Darwin in supplementation of his voluminous observations.

Following his pronouncements a vast literature of polemical writing appeared in which biologists and philosophers endeavored to express to the world what they thought of natural selection and of all other opinions on the subject.

The futility of mere discussion became apparent when de Vries, the experimental physiologist, entered the field presenting some new conceptions based on well-guarded cultures.

Phylogeny, evolution, and heredity were so vivified that researches were started in a hundred laboratories, and a dozen new journals are necessary for the publication of results.

It may be said that Weissmann's conception of germ plasm as the carrier of hereditary traits, invincible, inviolate and unmodifiable by environic causes, still holds, but only as conventional expression of the inertia of a strain of descent. Recent results, especially those obtained by subjecting organisms to the action of radiant energy of unaccustomed intensity or wave frequency, may destroy genes and alter linkages of characters causing breaks in transmission of hereditary characters of the most serious kind.

Practically all of the development of the study of bacterial organisms has been of a physiological character. The pathological action of these organisms on animals and man and crop plants has resulted in a development of this work into a separate branch with its own literature and laboratories, especially in pathology, in which fungi are also dealt with.

The separation has not gone so far, however, as to free the physiologist from his burden of understanding the action of soil bacteria and of fungi co-operating with the roots of higher plants in mycorrhizal arrangements.

Physiology has gone afield and quite literally in another manner in ecology. The study of organisms in a state of nature has been taken up by methods wholly new or materially modified from those which have been perfected in the laboratory. Physiology has thus been extended from the sea and the lakes, through swamps, fields, orchards, woods, plains and deserts to the mountain tops, with a development of many generalizations of the first rank.

Researches on the water-relations of plants have been widely extended in measuring transpiration, in the evaluation of the internal conditions and external agencies affecting the rate and amount. Attention directed to soil moisture and its use by the plant has resulted in a maze of literature of enormous volume. The wealth of facts recorded concerns almost all cultures, experimental or practical. The rate of loss, as well as the degree of hydration of the protoplasmic meshwork, affects almost all phases of metabolism and transformations of energy in the plant.

It is on the basis of these relations that water-loss is now taken to have been a prime factor in the evolutionary development of the higher plants, the ultimate expression of which is to be seen in the spinose and succulent forms of deserts.

The matter of the upward movement of sap has the distinction of a literature in which the essential problems were recognized two hundred and fifty years ago in the communications of Nehemiah Grew and of Malpighi to the Royal Society of London (1681). A little over two centuries ago (1727) Stephen Hales contributed notably to the subject, following which no contribution of enduring value was made until after the time of Sachs, although he and his co-workers and followers brought out a multitude of facts and a variety of explanations. The next notable advance was reported to the Royal Society in London by Dixon and Joly in 1895, this being the beginning of the development of the cohesion theory of the hydrostatic system of higher plants. The meshwork of water extending continuously from the

soil solutions wetting the root-hairs through the walls and lumina of vessels, tracheids, the colloidal masses of living cells in leaves terminating in ultra-microscopic meniscuses in the walls exposed to ventilated air spaces in the leaves, is the physical basis of this mechanism. The tensions set up by deformations in these surfaces may be as great as 200 atmospheres, and this pull is exerted on a meshwork of watery filaments capable of sustaining a stress of 300 pounds to the square inch. The configuration of this network or the path of sap varies widely with the morphology of the stems.

It is only since the time of Sachs that the transport of material from leaves or photosynthetic organs through petioles and stems to developing organs has been taken up seriously. No definite agreements have been reached as to the conduits, or the forces which are engaged. No comprehensive proposals have yet been made which can be taken as adequate to account for the amount and velocity of movement of the sugars, generally downward in the stem, although this subject has received the serious attention of some very able experimenters.

The amount and rate of upward flow of sap require the units of energy noted above, but it is also to be noted that the electrokinetic potential shows a gradient oriented to promote the flow in the xylem toward the apex of stems. Whether a reverse gradient found in the cortical region might be of importance in the movement of carbohydrates toward the base of the plant is a matter yet to be determined. The origin and nature of the so-called "root-pressure" is also undetermined after more than two centuries of observations and experiments.

The increases which are considered as growth in the broadest sense, the study of which received so much attention in Sachs' laboratory, have been for the most part dealt with by external measurements of one or two dimensions of organs, by total weight of individuals, by dry weight, or by counts of unicellular organisms. The approach is organogenic in any case. Studies of this character are essentially biographical, following the development of an individual or an organ from egg, parent cell or initial part way or on to maturity.

Earlier, the results were expressed in graphs showing the course

of growth plotted as velocities. During the last twenty-five years various efforts have been made to put the results into mathematical formulae. The rate of increase has been expressed in terms of the initial dry weight, and as compound interest on the initial dry weight.

Another view is that growth of an organ or individual may be given in the formula of an auto-catalytic reaction in which substance continuously secreted by the plant is the catalyst. The possibility of the identification of such a theoretical catalyst with the substance promoting fluidity or extensibility of the cell-walls is now meeting with some approval.

The analytical approach to the matter of growth is essentially that of Sachs who considered that division, elongation and differentiation are the stages from generative cells to permanent tissue. These three steps may now be characterized more closely as to the physical action involved.

During the first part of the existence of a new protoplast the dominant action is one of condensation of proteins and lipoids in a field near the iso-electric point nearly neutral or even slightly alkaline. The difference in this feature of the nucleus and of the cytoplasm is very slight. The entire protoplast has a low coefficient of hydration and permeability. Numerous very minute vacuoles are present which seem to have no connection with those that cause distention in the following stage.

With the attainment of full size, and seemingly consequent upon the movement of the chondriosomes from the neighborhood of the nucleus toward the periphery of the mass, a hysteresis or accumulation of solutions in vacuoles takes place. The osmotic action of these solut ons which may have a value of 75 or 80 atmospheres is now the distentive agency which may enlarge the cell to as much as a thousand times its initial volume at a rate presumably regulated by the special catalyst present. The amount of protoplasm remains but little changed; dry weight of walls and other solids increase greatly.

Some proteins are broken up and some mucilages are formed. Granular bodies appear in the cytoplasm and the cellulose wall is formed. The H ion concentration increases in both nucleus and cytoplasm, but most in the external layers so that in a dis-

tended parenchymatous cell the nucleus may show pH 5.5, and the outer part of the cell pH 4 to 4.5.

Whatever validity the equations of growth calculated on dry weight or volume supporting the auto-catalytic nature of growth may have will depend on their correct expression of the formation and action of the accessory substance which increases the extensibility of walls in the distending stage, as the change in volume in the initial stage and in the final differentiation forms a very low proportion of the total increase in volume.

Differentiation may be least in parenchymatous cells, or it may be carried to the extreme limits known to the anatomist, with the progressive consumption or wastage of the protoplast. The final disappearance of living matter from a cell leaves it in a condition where only mechanical uses are served, such as rigidity, or as conduits of solutions or gases.

The theory of Sachs as to specific organ-forming substances has been gradually modified, so that now it is taken for granted that construction is at the expense of general food-material, forming proteins and lipoids at first and carbohydrates later. His idea is now replaced by the conception of regulatory agents facilitating distention by increasing the fluidity or plasticity of cell-walls. There is also good evidence of the action of substances which retard growth by influencing condensation or distention.

Two major modifications of our conception of living matter have been made in the last two decades in addition to those disclosed in the studies of the mechanism of heredity. One is to the effect that protoplasmic units, such as those in meristematic layers, display no inherent rhythms except as enforced by variations in the environment. Thus no periodicities have been discernible in the cultures of cell-masses from embryo chicks by Carrel, which have been carried along for nearly two decades.

Likewise we know that growing points and sheets of cambium show no regularly recurring variations of their own. The variations displayed are all resultant from seasonal changes, maturation of permanent tissues, the depletion or repletion of the available food-supply, loss or cessation of function of such organs as leaves. In other words, periodicity in plants complies with the seasons or is organogenic, but not protoplasmic.

Our generalizations as to the inertia of protoplasm have also been modified by observations as to the durability of the delicately balanced mechanism of living material. It is now known that protoplasts may live for centuries. This is quite aside from scholastic discussions as to the immortality of primitive organisms in which death of the individual is replaced by its division into two others which, with their descendants, undergo scission instead of death.

In our own laboratories we have identified not only parenchymatous cells, but also other elements, such as wood-fibers, well on their way toward mature differentiation, in which the protoplasmic bodies retain an effective organization through several centuries. In some of the solid bodies there is fair certainty that the actual molecular meshwork has continuously existed without replacement. Buried seeds have shown similar longevity, and it is highly probable that these structures could be prepared to survive tens of centuries with their low rate of metabolism.

Progress in the study of the energetics of the green plant as pertaining to chlorophyll action and to the energy-releasing reactions under respiration may not adequately be described in a brief discussion. Since the discovery of respiration by green plants by Ingenhousz in 1774, and Rollo's detection of the excretion of carbon dioxide by plants in the absence of free oxygen, in what later was termed intra-molecular respiration, research has been directed to the identification of the substances which were subject to oxidation, and of the products. The first attempt at standardization in this field was in the determination of the oxygen-carbon dioxide quantitative relation or respiratory quotient. This has been found to be affected by a wide variety of agencies. The excretion of oxygen by green plants in light, discovered by Priestley in 1772, may be taken as the initial observation of photosynthesis, but the subject was not given its modern form until the time of Sachs. It seems to be agreed that Sachs is to be credited with the realization of the action of the chloroplasts, and that chlorophyll was formed only in the presence of light.

The last half century of research has included many attempts to identify the primary processes and products in respiration, and

photosynthesis. In neither field have there been achieved decisive results, although a great volume of information has been accumulated which may be expected to fall into place when a comprehensive theory of the implied activities is propounded.

The effort is now being made to determine the unit of radiant energy necessary to produce a certain effect in this process, which might become a general standard of measurement of energy exchange or transformation in the plant.

With the earlier development of methods, physiologists, in striving for precision, fell into the grave error of an extreme concentration on specific effects. Thus, for example, a certain intensity of illumination, a certain temperature, or some concentration of a mineral salt was supposed to have an unvarying effect; and this was sought in the praiseworthy urge for standardization. It has dawned but slowly on the physiologist that the causative action of any one agency is conditioned by the intensities of all other forces acting on the organism. All of these have a range from zero to an endurable maximum, and any one of them may become a "limiting factor" in a process or in an organogenic development.

Physiology attracted researchers of ability in Europe from the time of Sachs. Its recognition as a phase of botanical science in America came two decades later in America. Dr. J. C. Arthur appointed to the chair of plant pathology and physiology at Purdue University, and myself, appointed as assistant professor of botany in charge of plant physiology at the University of Minnesota in 1893, seem to have held the first research and teaching positions, although the subject was being presented in a few botanical departments elsewhere.

That the subject included the processes basic to agriculture dawned but slowly even in the most advanced agricultural colleges. Here it may be in charge of members of the staff holding the most diverse titles. Its contributions appear in a great number of journals of a range far beyond the direct interests of biological science.

The opportunities for research and the facilities for teaching have grown in pace commensurate with those in cognate sciences. Chairs, departments, and laboratories are numerous: some are well equipped.

The requirements of a laboratory which gives instruction and advanced work and offers opportunities for research are much greater than for a department of animal—often termed general—physiology. Instruments of precision, specially designed optical, physical, and chemical apparatus, chambers and glass houses, a stock of growing material and a garden of some sort, are among the indispensables as contrasted with the window-ledge experiments with lamp-chimneys, remodeled alarm clocks, tinware, and kitchen appliances of forty years ago.

Not the least important feature of my subject is that of the change in the relations of the experimental scientist to his fellow man and to society in the period under discussion. At its beginning "pure science" really meant "sterile learning," devoid of human interest. The world at large was not interested in the results gained in technical laboratories, which achieved publicity only when they seemed, to the lay mind, blasphemous, or as trespassing on the "secrets of nature."

The scientist reacted to such a set of environmental conditions with an attitude of disinterest in the practical implications of his findings. Science and life were utterly apart.

The contrast with to-day is worth a moment's consideration. Some of you will present results at New Orleans which will appear in newspapers with a million readers within the week and may perhaps be put on the cables for foreign readers. This ready recognition may come for a new theory on some phase of protoplasmic activity, or for methods of using known facts for the benefit of the race.

Increased appreciation of the importance of our studies calls for a full sense of our responsibilities. The interests of the plant physiologist run back to that early stage of living matter when chlorophyll, or other sun-screens, was first developed. The problems of life he seeks to solve are those which began to crowd the stage of the world consequent upon this direct utilization of the sun's energy: they concern the existence and continuation of the entire organic world.

The technology of any worker who may contribute to knowledge in this great field must be stark, precise, and as free of mysticism as of sentimentalism. He has no magic carpet, but

falls into the chasms encountered unless he succeeds in bridging them or passing on temporary or "false" work.

Vitalism is to him the ready recourse of baffled minds, unequal to the relentless demands of sound experimentation. That there may be forms of energy releases in living matter not yet recognizable, which, like the ultra-Plutonian planets, disturb calculations of the protoplasmic system, is admitted.

To our contemporaries, however, the physiologist has come to be known as a worker deeply immersed in a bewildering maze of phenomena. His entire attention is given to compilation of refined methods and systemization of results, with but little attempt at realization of the broader philosophical aspects of his subjects.

Plant physiology has developed a sound methodology for the study of living matter, its involutions, properties, performances in functions, organogenesis, heredity, and evolutionary development. It has for this half century drawn upon chemistry and physics in perfecting a technique which has been extended with great profit in genetics, bacteriology, and ecology. The utilization of its methods has been of incalculable advantage in agriculture and the plant industries.

Researchers in physiology have been regrettably content with the vast array of material facts secured by experimentation and have not carried their work toward a realization of the first principles or abstract possibilities of living matter and of the broader aspects of the organic world. Research is most worth while when it is a search for explanatory knowledge.

Philosophical considerations which look toward analytical explanations are as truly ours to use as our laboratory equipment. The restricted conclusions based on tests and measurements may have but small importance in comparison with a metaphysical aspect of the possibilities. The constructive value of a contribution is not to be determined by the mass of facts presented, not by the bricks and mortar, steel and concrete it furnishes, but by the architectural conceptions which may be realized by the use of these materials.

NEW OR OTHERWISE NOTEWORTHY APOCYNACEAE OF TROPICAL AMERICA. II[1]

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Allomarkgrafia Woodson, gen. nov. Apocynacearum (Echitoideae). Calyx profunde 5-partitus; laciniae subaequales scariaceae margine imbricatae basi intus multiglandulosae. Corolla speciosa infundibuliformis; tubus inferne anguste cylindricus dein circa medium staminiger et late campanulato-dilatatus numquam constrictus; limbi laciniae 5 aequales oblique obovato-reniformes aestivatione dextrorsum convolutae. Stamina 5 omnino inclusa; antherae inter se adglutinatae et stigmati adplicatae anguste oblongo-sagittatae basi obtuse biauriculatae dimidia parte superiore pollinigerae, sporangiis binis omnino fertilibus, pollinibus granulosis; filamenta subcylindrica brevissima saepissime retrorse pilosa. Ovarii carpella gemina basi distincta apice in stylo gracili producta, ovulis multis pluriseriatim superpositis; stigma fusiforme obscure 5-gonum apice obtusum. Nectarii glandulae 5 separatae vel basi plus minusve connatae. Fructus folliculares apocarpi tereti longe acuminati plus minusve falcati; semina numerosa subscaphoidea in longitudinem unisulcata apice bene comosa.—Frutices lactescentes volubiles; folia opposita petiolata subcoriacea integra penninervia, nervis principalibus basi ventro pluriglandulosis. Inflorescentia lateralis alternata multiflora omnino 2–3-chotome divisa, ramis bostrycino-racemosis divaricatis, pedicellis geminis unibracteatis.

Allomarkgrafia ovalis (Mgf.) Woodson, n. comb.

Echites ovalis Mgf. Notizblatt **9**: 79. 1924.

Echites ovalis Tafalla, ex Mgf. loc. cit. 1924, nom. nud. in synon.

The genus most closely allied to *Allomarkgrafia* is without doubt *Mesechites* Muell.-Arg., a valid group which has been generally ignored and confused with *Echites* P. Br., largely as a result of the efforts of John Miers in the past century. *Allomarkgrafia* has

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a large, infundibuliform corolla, whereas all the known species of *Mesechites* have much smaller, salverform corollas. The construction of the inflorescence is also diverse, that of the former genus being regularly branched with relatively distant, opposite pedicels, whereas that of the latter is characterized by irregular branching and extremely congested, indistinctly distributed pedicels. The foliar glands differ, furthermore, since those of the former are numerous and densely and indefinitely clustered, while those of the latter usually number but two or three and are regularly (either concentrically or radially) placed. A final and very important generic criterion is found in the number and disposition of the calycine squamellae, which are extremely numerous and uniformly distributed in *Allomarkgrafia*, and are only ten to fifteen in number and are placed strictly opposite the calyx-lobes in *Mesechites*.

The genus cannot be included within *Echites* P. Br. because of the obtusely auriculate anthers bearing uniformly fertile sporangia, the indeterminate inflorescence, and the foliar glands at the base of the midrib, which characterize it.

Allomarkgrafia has been so named in honor of Dr. Fr. Markgraf of the staff of the Botanical Museum at Berlin-Dahlem.

Asketanthera Woodson, gen. nov. Apocynacearum (Echitoideae). Calyx majusculis profunde 5-partitus; laciniae foliaceae plus minusve inaequales margine imbricatae intus basi squama deltoidea instructae. Corolla parva vel magna circa medium vel inferius 5-partita; tubus cylindricus infra medium staminiger; limbi aestivatione dextrorsum convoluti laciniae oblique ovato-lanceolatae. Stamina 5 inclusa; antherae in conum adglutinatae et stigmati adplicatae anguste ellipsoideo-oblongae basi acute bilobatae dimidia parte superiore pollinigerae, sporangiis binis basi in appendiculas rigidas productis, pollinibus granulosis; filamenta subcylindrica perbrevia saepissime pilosa. Ovarii carpella gemina basi distincta apice in stylo gracili producta, ovulis multis pluriseriatim superpositis; stigma fusiforme 5-gonum apice obscure bipartitum. Nectarii glandulae 5 saepissime separatae vel basi paulo connatae. Fructus folliculares apocarpi anguste tereti acuminati plus minusve falcati; semina numerosa sub-

scaphoidea in longitudinem unisulcata apice truncata vel paulo attenuata comosa.—Frutices lactescentes volubiles; folia opposita petiolata membranacea penninervia eglandulosa. Inflorescentia lateralis vel rarius subterminalis alternata bostrycino-racemosa bracteis foliaceis.

Asketanthera calycosa (A. Rich.) Woodson, n. comb.
Echites calycosa A. Rich. Fl. Cub. Fanerog. **2**: 94. 1853.
Rhodocalyx calycosus (A. Rich.) Miers, Apoc. So. Am. 140. 1878.
Echites Rugeliana Urb. Symb. Ant. **5**: 465. 1908.

Asketanthera dolichopetala (Urb.) Woodson, n. comb.
Echites dolichopetala Urb. Symb. Ant. **7**: 335. 1912.

Asketanthera longiflora (Ekm. & Helwig) Woodson, n. comb.
Echites longiflora Ekm. & Helwig, Ark. f. Bot. **22A**[10]: 45. 1929.

Asketanthera Picardae (Urb.) Woodson, n. comb.
Echites Picardae Urb. Symb. Ant. **5**: 466. 1908.

Asketanthera, a genus confined to the Greater Antilles, constitutes an extremely conspicuous and natural complexity of four species, as at present understood, each apparently endemic to a particular island or island group. *A. calycosa*, which is to be regarded as the type species, is limited to the island of Cuba, where it is of frequent and wide occurrence. *A. longiflora*, a native of Hispaniola, is more rare, and is noteworthy as bearing perhaps the largest and most beautiful flowers to be found among the Apocynaceae.

From *Echites* P. Br., with which it has its closest affinities both morphologically and geographically, *Asketanthera* differs markedly in the construction of the inflorescence, which is a compound, though frequently much reduced, dichasial cyme in the former, and a simple, bostrychoid raceme in the latter; in the character of the bracts and calyx-lobes, which are scarious and inconspicuous in the former genus, and foliaceous and extremely conspicuous in the latter; and in several more technical details of the repro-

ductive apparatus. The superficial dissimilarity of the genera is striking.

The generic name has been coined from ἀσκητός and ἀνθηρά, with reference to the highly modified stamens.

Fernaldia Woodson, gen. nov. Apocynacearum (Echitoideae). Calyx profunde 5-partitus; laciniae aequales vel subaequales margine imbricatae basi intus uniglandulosae. Corolla speciosa infundibuliformis; tubus inferne longe cylindricus supra medium late campanulato-dilatatus numquam constrictus ad basin partis dilatatae staminiger; limbi laciniae oblique obovatae aestivatione dextrorsum convolutae paulo reflexae in paginis ventralibus saepissime dense arachnoideo-villosae. Stamina 5 inclusa; antherae inter se adglutinatae et stigmati adhaerentes sagittatae anguste oblongo-ellipsoideae basi inconspicue obtuseque bilobatae parte dimidia superiore pollinigerae, sporangiis binis basi in appendiculas rigidas conspicue productis, pollinibus granulosis; filamenta brevia cylindrica glabriuscula. Ovarii carpella gemina basi distincta apice in stylo gracili producta, ovulis multis anatropis in utraque loculo pluriseriatim superpositis; stigma fusiforme obscure 5-gonum apice vix bipartitum. Nectarium cupuliforme inaequaliter 4-lobatum. Fructus folliculares apocarpi anguste cylindrici longe acuminati plus minusve falcati; semina numerosa subscaphoidea longitudinaliter unisulcata apice truncata bene comosa.—Frutices lactescentes volubiles; folia opposita petiolata margine integra penninervia eglandulosa. Inflorescentia lateralis rariusve subterminalis multiflora valde racemosa.

Fernaldia pandurata (A. DC.) Woodson, n. comb.

Echites pandurata A. DC. in DC. Prodr. **8**: 458. 1844.

Amblyanthera ? pandurata (A. DC.) Muell.-Arg. Linnaea **30**: 448. 1860.

Angadenia pandurata (A. DC.) Miers, Apoc. So. Am. 182. 1878.

Mandevilla velutina K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**[2]: 171. 1895.

Mandevilla potosina T. S. Brandg. Univ. Calif. Publ. Bot. **4**: 276. 1912.

Echites pinguifolia Standl. Field Mus. Publ. Bot. **8**: 35. 1930.

Although the infundibuliform corolla, racemose inflorescence, and bluntly auriculate anthers would appear superficially to ally *Fernaldia* to *Mandevilla* Lindl., it is actually more nearly related to *Echites* P. Br. This affinity is indicated by the eglandular foliage, the fusiform stigma, and the sporangia of the anthers, which are produced into a conspicuous, inwardly protuberant, sterile base.

From *Echites*, *Fernaldia* differs in the structure of the inflorescence, which is cymose in the former and racemose in the latter; in the shape of the corolla, which is salverform in the former and infundibuliform in the latter; in the anthers, which are produced into two sharp, basal prongs in the former, and are merely obtusely bilobed in the latter; and in the nectary, which is composed of five essentially equal and separate glands in the former genus, and is a cylindrical, irregularly four-lobed structure in the latter. *Fernaldia* differs from *Urechites* Muell.-Arg., furthermore, since it is without the terminally appendiculate anthers, the chaffy placentae, and the rostrate seeds which distinguish the latter genus. The arachnoid-villous corolla-lobes are without a parallel among the American Echitoideae.

The genus has been named in honor of Prof. Merritt Lyndon Fernald of the Gray Herbarium of Harvard University, who questioned the current generic interpretation of the type species while engaged in a study of the collections of Dr. Edward Palmer in southern Mexico.

Galactophora Woodson, gen. nov. Apocynacearum (Echitoideae). Calyx majusculis profunde 5-partitus; laciniae aequales vel subaequales margine imbricatae intus basi esquamuligerae sed saepissime glandulas minutas extra-axillares sparse munitae. Corolla magna speciosa; tubus inferne breviter cylindricus circa medium vel inferius late campanulato-dilatatus numquam constrictus ad basin partis dilatatae staminiger; limbi laciniae 5 aequales oblique obovatae aestivatione dextrorsum convolutae paulo reflexae. Stamina 5 omnino inclusa; antherae inter se plus minusve adglutinatae et stigmati adplicatae oblongo-lanceolatae sagittatae basi acute bilobatae parte dimidia superiore pollinigerae, sporangiis binis basi in appendiculas rigidas conspicue productis, pollini-

bus granulosis; filamenta subcylindrica brevissima pilosa. Ovarii carpella gemina basi distincta apice in stylo capillaceo longe producta, ovulis in utraque loculo pluriseriatim superpositis; stigma fusiforme obscure 5-gonum apice bipartitum. Nectarium cupuliforme apice obscure 5-lobatum. Fructus folliculares apocarpi anguste cylindrici longe acuminati plus minusve falcati; semina numerosa subscaphoidea in longitudinem unisulcata apice truncata ibique bene comosa.—Suffrutices erecti; folia opposita petiolata vel subsessilia saepe amplexicaulia coriacea penninervia eglandulosa. Inflorescentia terminalis bostrycino-racemosa pauciflora.

Galactophora crassifolia (Muell.-Arg.) Woodson, n. comb.

Amblyanthera crassifolia Muell.-Arg. in Martius, Fl. Bras. **6**[1]: 143. 1860.

Echites crassifolia Spruce, ex Muell.-Arg. loc. cit. 1860, nom. nud. in synon.

Rhodocalyx crassifolius (Muell.-Arg.) Miers, Apoc. So. Am. 139. 1878.

"*Mandevilla crassifolia* Muell.-Arg." ex K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**[2]: 171. 1895, sphalm.

"*Mandevilla crassifolia* (Spruce) K. Schum." ex Mgf. in Fedde, Rep. **20**: 24. 1924, sphalm.

Galactophora calycina (Hub.) Woodson, n. comb.

Dipladenia calycina Hub. ex Ducke, Archiv. Jard. Bot. Rio Janeiro **3**: 247. 1922; Bol. Mus. Goeldi **7**: 113. 1913, nom. nud.

Galactophora Schomburgkiana Woodson, sp. nov., suffrutescens; caulibus erectis teretibus sat crassis altitudine ignotis junioribus tenue glandulo-puberulis tandem glabratis; foliis oppositis subsessilibus paulo amplexicaulibus coriaceis margine in sicco revolutis late ovatis apice obtusiusculis basi subiter rotundatis et obscure cordatis 4–7 cm. longis 2.5–4.5 cm. latis supra tenuissime puberulis mox glabratis subtus glabris vel junioribus tenuissime puberulis; petiolis 0.1–0.2 cm. longis; inflorescentiis umbellatis paucifloris; pedunculis 3–5 cm. longis ut in caulis vestitis; pedicellis 1.0–1.5 cm. longis glandulo-puberulis et parce aculeolatis;

bracteis squamosis minimis; calycis laciniis ovatis acutiusculis 0.5–0.6 cm. longis scariaceis minutissime puberulis haud aculeolatis; corollae infundibuliformis extus minutissime glanduligerae in longitudinem aculeolato-striatae tubo 5–6 cm. longo basi ca. 0.2 cm. diametro metiente usque ½ altitudinem anguste cylindrico dein staminigero et campanulato-dilatato ostio ca. 0.75 cm. diametro metiente lobis oblique obovatis ca. 1 cm. longis; genitalibus ignotis; folliculis teretibus sat crassis ca. 14 cm. longis extus dense glandulo-aculeolatis.—BRITISH GUIANA: exact locality and date lacking. *R. Schomburgk s. n.* (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph).

Closely allied to *G. crassifolia* and *G. calycina*, but differing from both in the smaller calyx-lobes, which are but 0.5–0.6 cm. long and contrast sharply with those of the two related species which are 1.5–2.0 cm. long. The foliage, moreover, is ovate, whereas that of the allied species is broadly oblong. Because of the peculiar aculeolate emergences of the corolla, *G. Schomburgkiana* is considered to be more nearly related to *G. crassifolia*.

Galactophora pulchella Woodson, sp. nov., suffrutescens; caulibus erectis teretibus tenuibus altitudine ignotis junioribus minute puberulis tandem glabratis et lenticellas parvas gerentibus; foliis oppositis petiolatis subcoriaceis ovato-oblongis apice obtusiusculis basi subiter rotundatis vix cordatis 3.5–6.0 cm. longis 2.5–4.0 cm. latis supra glabratis subtus minutissime sparseque puberulis; petiolis 0.3–0.5 cm. longis glabris; inflorescentiis bostrycinoracemosis 5–10-floris; pedunculis 3–5 cm. longis ut in caulis vestitis; pedicellis ca. 0.75 cm. longis glabris vel minutissime glandulo-puberulis; bracteis scariaceis lanceolatis 0.15–0.2 cm. longis; calycis laciniis anguste lanceolatis 0.5–0.75 cm. longis scariaceis minute glandulo-puberulis et parce aculeolatis; corollae infundibuliformis glabrae vel paulo papillatae vix aculeolatae tubo 6–8 cm. longo basi ca. 0.2 cm. diametro metiente usque ¾ altitudinem anguste cylindrico dein staminigero et paulo ampliore tubuloso-dilatato ostio ca. 0.4 cm. diametro metiente lobis oblique ovato-oblongis obtusiusculis 1.0–1.25 cm. longis paulo reflexis; antheris anguste lanceolatis 0.5–0.6 cm. longis basi acutissime auriculatis dorso minute puberulo-papillatis; nectario cupuliformi apice 5-lobato ovariis oblongoideis glabris paulo breviore; folliculis igno-

tis.—BRAZIL: Cano Pimicheiro, June, 1854. *R. Spruce 3718* (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Distinctive because of its narrowly tubular corolla-throat and lanceolate calyx-lobes. It is also the only species of the genus with foliage which is not amplexicaul.

The type specimens of the two species immediately preceding were found in the collection of undetermined Apocynaceae at the Herbarium of the Royal Botanic Gardens, Kew. Both are evidently unicates, as duplicates have been encountered in none of the other European or American herbaria which have been consulted during the course of these studies.

Galactophora is a genus apparently without any direct affinity among the genera of its subfamily. Because of its esquamuliferous calyx and infundibuliform corolla, it is thought that *Rhabdadenia* may be considered as closely allied. The two genera, however, are of entirely different habit, *Rhabdadenia* consisting of extensive lianas for the most part, and *Galactophora* of low, suffrutescent undershrubs. The nectaries of the former genus are essentially separate, moreover, whereas those of the latter are completely concrescent. Furthermore, the seminal coma of *Rhabdadenia* is borne upon a slender rostrum, while that of *Galactophora* is sessile. The glandular-aculeolate emergences of the corolla, calyx, and stems of the latter genus are unique in the entire family as at present understood. The provenience of the Latin designation is obvious.

Mandevilla tubiflora (Mart. & Gal.) Woodson, n. comb.

Echites tubiflora Mart. & Gal. Bull. Acad. Roy. Brux. **11**: 358. 1844.

Amblyanthera tubiflora (Mart. & Gal.) Muell.-Arg. Linnaea **30**: 423. 1860.

Echites Cobanensis Donn.-Sm. Bot. Gaz. **40**: 6. 1905.

What is evidently the sole surviving specimen of Galeotti's original collection (no. *1579*) has recently been discovered among the undetermined Apocynaceae in the herbarium of the Royal Botanic Gardens, Kew, and discloses the corolla of this species to be typically salverform, with a conspicuous, spreading limb.

Another species, collected upon several occasions by C. G. Pringle and Dr. Edward Palmer in southern Mexico and widely distributed as *Echites tubiflora* Mart. & Gal., is characterized by an almost precisely tubular corolla, with an inconspicuous, erect limb, and appears to constitute a novelty:

Mandevilla Syrinx Woodson, sp. nov., suffruticosa volubilis; ramulis gracilibus juventate puberulis tandem glabratis; foliis oppositis breviter petiolatis membranaceis elliptico-ovatis vel oblongo-lanceolatis plerisque profundiuscule cordatis apice imo in acumen breve constrictis supra hispidulis glabratisve nervo medio basi pluriglandulosis subtus pallidioribus tomentulosis vel rarius laxe pilosis 5–14 cm. longis 1.5–8.0 cm. latis; petiolis 0.5–1.0 cm. longis puberulis; inflorescentiis racemosis lateralibus vel subterminalibus alternatis multifloris; pedunculo foliis subaequante ut in ramulis vestito; pedicellis congestis subsecundis 0.3–0.5 cm. longis; bracteis ovato-lanceolatis linearibusve scariaceis pedicellis subaequantibus; calycis laciniis ovatis vel ovato-lanceolatis acuminatis 0.3–0.5 cm. longis scariaceis extus minute puberulo-papillatis intus basi squamellas multas flagelliformes uniforme munitis; corollae tubiformis dilute flavidulae tubo cylindrico 0.5–0.75 cm. longo basi ca. 0.2 cm. diametro metiente circa medium vel inferius staminigero faucibus paulo ampliatis lobis late ovatis acutiusculis erectis ca. 0.4 cm. longis; antheris anguste oblongo-lanceolatis basi truncate auriculatis 0.4 cm. longis; ovariis late ovoideis dense puberulo-papillatis apice in stylo abrupte contractis 0.2 cm. longis; stigmate proprio 0.2 cm. longo apiculis paulo breviore; nectarii glandulis oblongoideis plus minusve distinctis ovariis aequantibus vel paulo superantibus; folliculis falcatis glabris haud articulatis 15–25 cm. longis; seminibus ca. 0.1 cm. longis como dilute flavido dimidio brevioribus.—MEXICO: Jalisco: barranca of Tequila, Oct. 8, 1893. *C. G. Pringle 5422* (Mo. Bot. Garden Herbarium, TYPE).

A number of collections of this species has already been made in the Mexican states of Jalisco, Michoacan, Morelos, Guanajuato, and Oaxaca, representing a considerable degree of variation in such characters as the foliar indument and the length and degree of attenuation of the calyx-lobes. Without field observation,

or, at any rate, still more ample specimens, however, it has been decided to forego the creation of a number of intergrading varieties.

The curiously erect limb of the corolla, combined with the strikingly compact, subsecund inflorescence, has suggested as a substantive adjective for the species the name of the familiar wind instrument of the classical Greeks.

Mandevilla acutiloba (A. DC.) Woodson, n. comb.
Echites acutiloba A. DC. in DC. Prodr. **8**: 451. 1844.
Amblyanthera acutiloba (A. DC.) Muell.-Arg. Linnaea **30**: 426. 1860.

The original specimen of *M. acutiloba* collected by Pavon and now incorporated within the Herbier Boissier at Geneva is without data concerning locality. A specimen in the United States National Herbarium, collected in the state of Chiapas, Mexico, near Tumbala, by E. W. Nelson (no. *3337*), however, coincides well with that of Pavon, and might be assumed to have come from approximately the same general region. In any event, it appears evident that the latter is either Mexican or Central American in origin, since it possesses the hypogynous nectaries equalling or slightly surpassing the ovary, the long-apiculate stigma, and the blunt anther-lobes characteristic of the salverform-flowered Mexican and Central American species of the subgenus *Eumandevilla*. All known South American species of *Eumandevilla* bearing salverform corollas have nectaries surpassed by the ovary, shortly apiculate stigmata, and anthers which are without basal lobes. It is extremely unfortunate that the species is as yet represented by but two specimens among the principal herbaria of both Europe and America.

Mandevilla Donnell-Smithii Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracilibus dense puberulis; foliis oppositis petiolatis membranaceis late ovatis vel ovato-oblongis profunde cordatis apice breviter acuminatis 4–10 cm. longis 2–8 cm. latis supra viridibus dense hirtellis nervo medio basi pluriglandulosis subtus pallidioribus tomentosis; petiolis 0.75–3.0 cm. longis tomentulosis; inflorescentiis racemosis lateralibus alternatis

10–25-floris; pedunculo foliis aequante vel paulo superante ut in ramulis vestito; pedicellis secundis plus minusve congestis 0.5–0.75 cm. longis; bracteis scariaceis anguste lanceolatis 0.2–0.5 cm. longis; calycis laciniis scariaceis ovatis vel oblongo-lanceolatis acuminatis 0.2–0.4 cm. longis extus obscure puberulis intus basi pluriglandulosis; corollae salverformis dilute flavidae tubo cylindrico 1.25–1.5 cm. longo basi ca. 0.15 cm. diametro metiente supra medium staminigero faucibus paulo ampliatis lobis oblique obovatis obtusiusculis patentibus 0.25–0.4 cm. longis; antheris ovatis vel late oblongis basi truncate auriculatis 0.4 cm. longis; ovariis ovoideis apice subiter constrictis ca. 0.15 cm. longis glabris; stigmate proprio ca. 0.1 cm. longo apiculis sterilibus subaequante; nectarii glandulis oblongo-ovoideis plus minusve distinctis ovariis aequantibus vel eadem paulo superantibus; folliculis ignotis.—GUATEMALA: Dept. Santa Rosa: Cerro Gordo, alt. 3500 pp., Aug., 1892. *H. T. Heyde & E. Lux 3993* (Gray Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Superficially, *M. Donnell-Smithii* may be distinguished from *M. tubiflora*, with which it is most likely to be confused, by means of its secund inflorescence and somewhat broader foliage. Technical details of the reproductive organs also vary. The species is evidently widespread in Guatemala, where it is a liana of mountain forests, frequenting altitudes of 1000 to 2500 meters.

Mandevilla platydactyla Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracilibus juventate ferrugineo-tomentulosis tandem glabratis maturitate lignosis in longitudinem leviter striatis; foliis oppositis breviter petiolatis membranaceis obovato-oblongis apice abrupte acuminatis basi cuneatis obscure angusteque cordatis plerisque 5–10 cm. longis 2.5–5.0 cm. latis supra minute hispidulis nervo medio basi pluriglandulosis subtus pallidioribus praecipue in nervis venisque dense ferrugineo-tomentosis; petiolis 0.2–0.4 cm. longis ut in pagina ventrali folii vestitis; inflorescentiis racemosis lateralibus alternatis 10–25-floris; pedunculo foliis subaequante ut in ramulis vestito; pedicellis laxis plus minusve reflexis 0.8–1.0 cm. longis; bracteis oblongis acuminatis 0.3–0.6 cm. longis scariaceis sparse pilosis; calycis laciniis majusculis obovato-oblongis breviter acuminatis 0.75–1.0

cm. longis scariaceis (ante exsiccationem plus minusve coloratis ?) extus ferrugineo-puberulis intus basi squamellas multas dentiformes munitis; corollae (in sicco aurantiacae) salverformis tubo cylindrico 1.25–1.5 cm. longo basi ca. 0.3 cm. diametro metiente supra medium constricto ibique staminigero faucibus paulo ampliatis lobis oblique ovato-oblongis acutiusculis patentibus 0.4 cm. longis; antheris anguste oblongis basi truncate auriculatis 0.4 cm. longis; ovariis ovoideis apice abrupte constrictis 0.4–0.5 cm. longis pilosulis; stigmate proprio ca. 0.1 cm. longo apiculis subaequante; nectarii glandulis ovoideis plus minusve connatis ovariis subaequantibus; folliculis ignotis.—MEXICO: Hidalgo (?): Tolapa, June, 1842. *F. M. Liebmann 11986* (Herbarium, Botanical Museum of Copenhagen, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

This species is one of the most striking of the Mexican representatives of the subgenus *Eumandevilla*. Because of its salverform corolla with conspicuous, spreading limb, and stamens inserted somewhat above midway within the tube, it is thought to be most closely allied to the series of species centering about *M. tubiflora*, *M. acutiloba*, and *M. Donnell-Smithii*, but differs from all in the showy development of the calyx, the lobes of which are broadly laminate and probably somewhat tinted in the living condition.

Mandevilla Rosana (Donn.-Sm.) Woodson, n. comb.

Echites Rosana Donn.-Sm. Bot. Gaz. **40**: 6. 1905.

At present known only from the type locality in Guatemala, this species differs from *M. acutiloba*, which might be regarded as its nearest congener, in the insertion of the stamens almost exactly midway within the corolla-tube, in the ovate lobes of the corolla, and in the somewhat rounded anther-lobes.

Mandevilla scorpioidea Woodson, sp. nov., suffruticosa volubilis; ramis teretibus gracilibus dense hirtellis; foliis oppositis longiuscule petiolatis membranaceis ovato-oblongis cordatis apice acuminatis 5–12 cm. longis 2.0–5.5 cm. latis supra hispidulis nervo medio basi pluriglandulosis subtus vix pallidioribus leviter puberulis; petiolis 0.5–1.0 cm. longis minute hirtellis; inflores-

centiis racemosis lateralibus alternatis 20–30-floris; pedunculo folia bis terve superante ut in ramis vestito; pedicellis sparsis subsecundis 0.75–1.0 cm. longis; bracteis linearibus 0.5–0.7 cm. longis pilosulis; calycis laciniis ovato-lanceolatis longe acuminatis 0.4–0.5 cm. longis scariaceis extus minute puberulo-papillatis intus pluriglandulosis; corollae (flavidae ?) salverformis tubo cylindrico 1.5 cm. longo basi ca. 0.15 cm. diametro metiente circa medium vel inferius staminigero deinde paulo dilatato fauces versus parum attenuato lobis oblique ovatis obtusiusculis patentibus 0.4–0.5 cm. longis; antheris lanceolatis basi rotundiuscule auriculatis 0.4 cm. longis; ovariis ovoideis apice abrupte constrictis ca. 0.1 cm. longis glabris; stigmate proprio ca. 0.1 cm. longo apiculis ca. ⅓ breviore; nectarii glandulis oblongoideis distinctis ovariis aequantibus; folliculis ignotis.—MEXICO: Chiapas: Cerro del Boqueron, June, 1914. *C. A. Purpus 7274* (Mo. Bot. Garden Herbarium, TYPE).

A species of very distinct aspect due to the long, subsecund inflorescence. The insertion of the stamens about midway within the corolla-tube appears to indicate a closer relationship to *M. Rosana* than to any other species at present known from Mexico or Central America.

Mandevilla scutifolia Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracillimis minute puberulis; foliis oppositis petiolatis membranaceis late ovato-oblongis apice breviter acuminatis mucronulatis basi rotundatis obsolete cordatis 2–5 cm. longis 1.5–3.0 cm. latis supra minute puberulis nervo medio basi pluriglandulosis subtus vix pallidioribus in nervis laxe barbatis; petiolis 1.0–1.25 cm. longis minutissime puberulo-incanis; inflorescentiis racemosis lateralibus alternatis 3–10-floris; pedunculo foliis subaequante dimidia parte inferiore sterili deinde florifero ut in ramulis vestito; pedicellis laxis 0.75–1.0 cm. longis; bracteis ovato-oblongis acuminatis 0.3–0.4 cm. longis scariaceis; calycis laciniis ovatis acutiusculis 0.3 cm. longis scariaceis extus minute denseque puberulis intus basi in marginibus squamellas 3–4 flagelliformes munitis; corollae (gilvae) salverformis tubo gracile cylindrico 1 cm. longo basi ca. 0.1 cm. diametro metiente circa medium staminigero faucibus paulo ampliatis lobis oblique obo-

vato-reniformibus obtusiusculis patentibus 0.5 cm. longis; antheris oblongo-lanceolatis basi truncatis haud auriculatis 0.35 cm. longis; ovariis oblongo-ovoideis apice gradatim constrictis 0.1 cm. longis omnino glabris; stigmate proprio 0.2 cm. longo apicula terminalia ca. bis superante; nectarii glandulis ovoideis compressis truncatis plus minusve connatis ovariis dimidio aequantibus; folliculis ignotis.—PERU: "Andes of Saragosa," date lacking. *W. Lobbs. n.* (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

While its affinities are clearly with the other South American species of *Eumandevilla* bearing salverform corollas, the distinct structure of the inflorescence, which might almost be described as subumbellate, as well as the size and shape of the corolla, entitles *M. scutifolia* to a unique position, without any very closely neighboring congeners. The species is known at present only from the type collection.

Mandevilla riparia (HBK.) Woodson, n. comb.

Echites riparia HBK. Nov. Gen. 3: 214. 1818.

The generic affinities of this plant, collected in recent years, as originally, in the valley of the Magdalena River of Colombia, are obviously with *Mandevilla* by reason of the glandular foliage, simple, racemose inflorescence, and umbraculiform stigma. It differs from *M. montana* (HBK.) Mgf. chiefly in the longer, more slender corolla-tube with orbicular-ovate lobes, and in the shorter calyx.

Mandevilla Jamesonii Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus crassiusculis juventate minute puberulis mox glabratis; foliis oppositis petiolatis membranaceis late ovato-oblongis apice breviter acuminatis basi rotundatis et obsolete cordatis 3–6 cm. longis 2–4 cm. latis supra subpuberulis glabratisve nervo medio basi pluriglandulosis subtus pallidioribus molliter puberulis; petiolis 0.75–1.0 cm. longis laxe pilosulis; inflorescentiis racemosis lateralibus vel subterminalibus alternatis ca. 6-floris; pedunculo puberulo foliis subaequante; pedicellis 1.25 cm. longis laxis; bracteis lanceolatis ca. 0.2 cm. longis scariaceis; calycis laciniis lanceolatis acuminatis 0.4–0.5 cm. longis

scariaceis extus puberulis intus basi in marginibus squamellas 4–5 flagelliformes instructis; corollae (ut videtur gilvae) salverformis tubo gracile cylindrico 2 cm. longo basi ca. 0.15 cm. diametro metiente circa medium staminigero et paulo dilatato lobis oblique obovatis dolabriformibusque apice rotundatis patulis tubo subaequantibus; antheris anguste oblongo-lanceolatis 0.5–0.6 cm. longis basi haud auriculatis; ovariis oblongo-ovoideis apice in stylo gradatim constrictis 0.2 cm. longis glabris; stigmate proprio ca. 0.25 cm. longo apiculis subaequantibus; nectarii glandulis ovato-quadratis plus minusve connatis ovariis ca. duplo brevioribus; folliculis ignotis.—ECUADOR: "hedges, Loxa," date lacking. *W. Jameson 153* (Herbarium Kew, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Although closely allied to the other South American species of the *montana* plexus of *Eumandevilla*, *M. Jamesonii* is conspicuous because of the magnitude of the flowers and the elaborate coroline limb.

Mandevilla subsessilis (A. DC.) Woodson, n. comb.

Echites subsessilis A. DC. in DC. Prodr. **8**: 451. 1844.

This is certainly one of the most peculiar species of *Mandevilla*. Its unusually large, broadly obovate, sessile or subsessile, amplexicaul leaves, and clumsy, obovate-reniform calyx-lobes are quite different from those of any other species of the genus known at present. Technical details, however, prove it correctly referable to the group of South American species of *Eumandevilla* centering about *M. montana* (HBK.) Mgf., thus fortunately judging the doubtful data "*Mexico ? Peruvia ?*" upon Pavon's original specimen in the Herbier Boissier. The plant has evidently been collected but once.

Mandevilla fragilis Woodson, sp. nov., suffruticosa volubilis; ramis teretibus gracilissimis juventate minute sparseque puberulis mox glabratis; foliis oppositis petiolatis tenuiter membranaceis anguste oblongo-lanceolatis acuminatis obsolete cordatis 3–7 cm. longis 0.75–1.5 cm. latis supra glabris nervo medio basi pauciglandulosis subtus glaucis; petiolis 0.75–1.25 cm. longis omnino glabris; inflorescentiis racemosis lateralibus alternatis 3–5-floris;

pedunculo glabro foliis paulo breviore; pedicellis laxis 0.75–1.0 cm. longis; bracteis minimis scariaceis; calycis laciniis ovato-oblongis acutiusculis 0.1 cm. longis scariaceis extus glabris intus basi in marginibus squamellam flagelliformem instructis; corollae (flavidae plus minusve roseatae ?) fragilis salverformis tubo cylindrico gracilissimo 1.25 cm. longo basi ca. 0.1 cm. diametro metiente circa medium staminigero sed vix dilatato, lobis inaequilateraliter ovato-oblongis acutiusculis valde patentibus tubo vix aequantibus; antheris anguste oblongis basi truncatis haud auriculatis 0.3 cm. longis; ovariis oblongo-ovoideis ca. 0.05 cm. longis apice in stylo capillaceo gradatim attenuatis omnino glabris; stigmate proprio 0.2 cm. longo apicula sterilia ca. bis superante; nectarii glandulis ovoideis ovariis vix aequantibus; folliculis ignotis.—BOLIVIA: exact locality and date lacking. *M. Bang 2271* (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

This delicate and exceedingly graceful species is peculiar because of the solitary squamellae alternating with the lobes of the calyx. In its habit, it has no counterpart in the genus as at present understood.

Mandevilla pycnantha (Steud.) Woodson, n. comb.

Echites densiflora Pohl, ex Stadelm. Flora **24**: Beibl. I. 56. 1841, not Blume.

Echites pycnantha Steud. Nom. ed. 2. **1**: 540. 1841.

Heterothrix pycnantha (Steud.) Muell.-Arg. in Martius, Fl. Bras. **6**[1]: 133. 1860.

Apparently only two collections have ever been made of this puzzling species: one bearing flowers only, by Riedel (no. *985*) at the Serra da Lapa, southern Brazil, and represented in the herbaria of the Jardin de l'Etat, Brussels, the Royal Botanic Gardens, Kew, the Botanical Museum, Vienna, and the Gray Herbarium of Harvard University, Cambridge; and another, bearing fruit only, by Pohl at the Serra do Pinheiro, in the state of Minas Geraes, Brazil, and represented at Brussels and Vienna only.

Mueller-Argoviensis regarded the plants as constituting a monotypic genus, *Heterothrix*, separating them from *Amblyan-*

thera Muell.-Arg., not Blume (antedated by *Mandevilla* Lindl.), upon the supposition of a seminal coma consisting of two distinct series of hairs. When examining the fruiting specimens collected by Pohl, the writer was disappointed to find the follicles nearly empty, with only the tangled masses of the yellow coma twisted and matted among the several mericarps. After rather laborious extraction of numerous strands, some of which were fortunately yet attached to seeds, it has been assumed that the coma of *M. pycnantha* is probably similar to that of all other known Echitoideae in being homogeneous. The observation of Mueller is thought to have been affected by the fragmentary and grossly distorted material available for his study. With its only generic character held in serious question, therefore, the species has been placed provisionally within *Mandevilla* subgen. *Eumandevilla* with the technical criteria of which it appears to coincide in every essential respect.

Mandevilla cercophylla Woodson, sp. nov., suffruticosa volubilis omnino glabra; ramulis subteretibus gracilibus; foliis oppositis longiuscule petiolatis subcoriaceis obovato-oblongis apice abrupte acuminatis subcaudatis basi gradatim angustatis et obsolete auriculatis 3–6 cm. longis 1–3 cm. latis nervo medio basi ventro pauciglandulifero nervis secundariis fere horizontalibus haud arcuatis distantibus prope marginem junctis; petiolo 0.5 cm. longo; inflorescentiis racemosis lateralibus alternatis 8–17-floris; pedunculo flexuoso foliis subaequante; pedicellis laxis 0.75–1.0 cm. longis; bracteis ovatis minimis scariaceis; calycis laciniis ovato-trigonalibus ca. 0.1 cm. longis scariaceis intus basi squamellas multas flagelliformes gerentibus; corollae salverformis colore ignotae tubo cylindrico gracillimo 1.25 cm. longo basi ca. 0.1 cm. diametro metiente circa medium staminigero sed haud distincte dilatato lobis oblique ovato-oblongis acutiusculis (erectis vel vix patentibus ?) 0.5 cm. longis; antheris lanceolatis basi truncatis haud auriculatis 0.45 cm. longis; ovariis oblongo-ovoideis 0.15 cm. longis apice in stylo gracillimo gradatim productis; stigmate proprio 0.15 cm. longo apiculis terminalibus vix aequante; nectarii glandulis oblongo-ovoideis basi connatis ovariis dimidio aequantibus; folliculis maturis ignotis.—PERU: Casapi, date lacking.

A. Matthews 1978 (Herbarium Kew., TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Probably as closely allied to *M. brachyloba* (Muell.-Arg.) K. Sch. as to any other species known at present, because of the short corolla-lobes which are thought to have been erect or essentially so in the living condition. The corolla is without the glandular papillae characteristic of that of *M. brachyloba*, however, and consequently does not blacken upon desiccation as does the corolla of the latter species. The leaves, moreover, are subcoriaceous, caudate-acuminate, obscurely auriculate, and are characterized by horizontal secondary venation, in all quite dissimilar to the foliage of *M. brachyloba*. The plant has evidently been collected but once.

Mandevilla erecta (Vell.) Woodson, n. comb.

Echites erecta Vell. Fl. Flum. 113. 1830; Icon. **3**: *pl. 45*. 1827.

Laseguea erecta (Vell.) Muell.-Arg. in Martius, Fl. Bras. **6**[1]: 135. 1860.

Originally established with two species of dubious distinction, the genus *Laseguea* appears to differ from most other American Echitoideae in the conspicuous, brushy inflorescence, bearing subtubular corollas with small, erect lobes scarcely surpassing the curiously foliaceous bracts and calyx-lobes. The plants referred to *Laseguea* are surely very conspicuous, and have been popular with both collectors and systematists for that reason.

Mueller-Argoviensis was evidently hard put to assure the integrity of the genus *Laseguea* by ascribing to it more precise morphological criteria than those of vegetative habit, and made the observation of a dissimilar seminal coma as he had interpreted in the case of the genus *Heterothrix*. In spite of Mueller's definition of the coma, however, the foliaceous bracts and calyx-lobes and salverform corolla, accompanied by reasonably broad foliage, have remained the real distinction of the genus as popularly conceived.

These features, supposedly distinctive of *Laseguea*, were eventually proved invalid by John Miers, in an unintentional *reductio ad absurdum*, by applying the name to every species,

from Mexico to southern Brazil, which could possibly be so interpreted by the characters of the inflorescence alone. K. Schumann, in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 171. 1895, may have criticized rather unjustly, therefore, when he wrote: "Auch in dieser Gattung [*Laseguea*] hat Miers viel mehr Arten aufgezählt; ich möchte fast glauben, dass er alle Echitoideae mit grossen Kelchen mehr dem Zufall als einem bestimmten Princip nach unter Laseguea und Rhodocalyx aufgeteilt hat," for he himself was unable to suggest more definite criteria.

When examined critically, the distinguishing characters of *Laseguea* quickly resolve into a combination of features present in numerous species of *Mandevilla*. The corolla of the former, which is tubular or subtubular with an inconspicuous, erect limb, occurs in almost exact proportions in *M. brachyloba* and *M. cercophylla*, also of South America. As in the former, the exterior of the corolla is densely studded with minute, glandular papillae; but as in the latter, desiccation is not accompanied by blackening.

The conspicuous calyx-lobes and bracts of *Laseguea*, moreover, are equalled or even surpassed in magnitude by those of several species of *Mandevilla*, a particular instance of timely note being *M. platydactyla* newly described in a preceding paragraph of these records. The bracts of several Mandevillas, in particular, are even more striking than those of *Laseguea*, as, for example, those of *M. villosa* (Miers) Woodson, *M. bracteata* (HBK.) K. Sch., and *M. javitensis* (HBK.) K. Sch. When considered independently, the essential organs of the flower and foliage are all indistinguishable from those of *Mandevilla* subgen. *Eumandevilla*, to which *Laseguea* with its two valid species is relegated. Abundant fruiting material again has failed to reveal the foundation of Mueller's observation of a double coma.

Mandevilla Pentlandiana (A. DC.) Woodson, n. comb.

Parsonsia ? bracteata Hook. & Arn. in Hook. Jour. Bot. **1**: 287. 1834.

Laseguea Pentlandiana A. DC. Ann. Sci. Nat. Bot. III. **1**: 262. 1844.

Laseguea Hookeri Muell.-Arg. in Martius, Fl. Bras. 6^1: 136. 1860.

Laseguea bracteata (Hook. & Arn.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 171. 1895.

Laseguea Mandoni Britton, ex Rusby, Mem. Torrey Bot. Club 4: 220. 1895.

One may question very justly the distinction between *M. Pentlandiana* and *M. erecta*. The former is composed apparently of rather extensive sylvan lianas of Bolivia and northern Argentina, and is characterized by distinctly petiolate, ovate-cordate foliage. On the other hand, *M. erecta* is represented by more or less erect, suffrutescent undershrubs with nearly sessile, orbicular-ovate leaves, apparently being found only on the campos of Paraguay and adjoining Brazil and Uruguay. As a matter of fact, the delimitation of Apocynaceous lianas and undershrubs is not particularly precise, especially among the Echitoideae of southeastern South America; and with additional study and accumulation of specimens, the two species may be found to merge.

The type specimen of *Laseguea Pentlandiana* A. DC. was not found for examination in the Herbier Boissier as indicated by de Candolle, but the original description coincides well with plants examined in the course of these studies. It is interesting to note, furthermore, that according to de Candolle the specimen collected by Pentland upon which the species was based bears the data "*In Bolivia, ad Illimani.*" *Buchtien 250*, occurring in several of the principal herbaria of America and Europe, was also collected in Bolivia, bearing the data "*Cotana am Illimani,*" and may therefore be viewed as virtually a topotype. The earlier specific name of Hooker and Arnott cannot be used in this combination because of the pre-existence of *M. bracteata* (HBK.) K. Sch.

Mandevilla torosa (Jacq.) Woodson, n. comb.

Echites torosa Jacq. Enum. Syst. Pl. Carib. 13. 1760.

Echites torulosa L. Sp. Pl. ed. 2. 307. 1762.

Echites torosa Jacq. var. *Brownei* A. DC. in DC. Prodr. 8: 449. 1844.

Amblyanthera torosa (Jacq.) Muell.-Arg. Linnaea 30: 446. 1860.

Echites Brownei (A. DC.) Muell.-Arg. loc. cit. 1860.

Mesechites torulosa (L.) Miers, Apoc. So. Am. 229. 1878.
Mesechites Brownei (A. DC.) Miers, loc. cit. 232. 1878.

The affinities of this species were recognized by Mueller, but *Amblyanthera* is a generic name not only antedated by *Mandevilla* Lindl., but invalidated by a previous homonym. The plant is a native of Jamaica where it constitutes a very clear-cut and uniform species and is the only representative of the genus in the Antilles. It is also found in Yucatan, but there becomes rather aggregate and variable, probably through hybridization with the closely related *M. Karwinskii* (Muell.-Arg.) Hemsl. A distribution common to Jamaica and northern Yucatan is not infrequent among the Apocynaceae.

Mandevilla mexicana (Muell.-Arg.) Woodson, n. comb.
Amblyanthera mexicana Muell.-Arg. Linnaea **30**: 424. 1860.
Echites mexicana (Muell.-Arg.) Miers, Apoc. So. Am. 205. 1878.
Echites Smithii Greenm. Proc. Am. Acad. **40**:29. 1904.

Closely related to *M. foliosa* (Muell.-Arg.) Hemsl., and differing chiefly in the size and indument of the foliage.

Mandevilla apocynifolia (A. Gray) Woodson, n. comb.
Echites (*Amblyanthera ?*) *apocynifolia* A. Gray, Proc. Am. Acad. **22**: 435. 1887.

That Dr. Gray suspected the generic affinities of this species is indicated by his dubious, parenthetical reference to the invalid genus *Amblyanthera* Muell.-Arg. *M. apocynifolia*, together with *M. mexicana*, *M. foliosa* (Muell.-Arg.) Hemsl., and *M. Karwinskii* (Muell.-Arg.) Hemsl., constitutes a conspicuous group, probably deserving of sectional rank, which is characterized by an extremely suffrutescent, virtually herbaceous, erect habit. The species of this group intergrade through occasionally twining individuals of *M. Karwinskii* and the typically volubile *M. torosa* to the liana habit characteristic of the bulk of species of the genus.

Mandevilla equatorialis Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracillimis juventate minute puberulis tandem glabratis; foliis oppositis petiolatis rigide membranaceis

ovato-oblongis breviter acuminatis obscure lateque cordatis plerisque 2–5 cm. longis 1.0–1.25 cm. latis supra minute puberulis mox glabratis nervo medio basi pauciglanduliferis subtus pallidioribus et dense tomentellis; petiolis 0.3–0.7 cm. longis puberulis; inflorescentiis racemosis lateralibus vel subterminalibus alternatis 8–14-floris; pedunculo puberulo folia ca. duplo superante; pedicellis laxis 0.4 cm. longis post maturitatem paulo accrescentibus; bracteis lanceolatis 0.2–0.3 cm. longis scariaceis; calycis laciniis lanceolatis acuminatis 0.2 cm. longis scariaceis extus minute puberulo-papillatis intus basi in marginibus squamellas 3–5 flagelliformes gerentibus; corollae (gilvae vel purpurascentis ?) infundibuliformis extus minute puberulae tubo proprio cylindrico brevissimo 0.2 cm. longo basi ca. 0.1 cm. diametro metiente ad apicem staminigero deinde angustiuscule conico-dilatato faucibus 0.5–0.7 cm. longis ostio ca. 0.4 cm. diametro metiente lobis oblique ovato-lanceolatis acuminatis 0.3 cm. longis; antheris anguste oblongis basi truncatis haud auriculatis 0.35 cm. longis; ovariis ovoideis ca. 0.1 cm. longis apice in stylo gracili gradatim attenuatis glabris; stigmate proprio ca. 0.15 cm. longo apiculis sterilibus vix aequante; nectarii glandulis ovoideo-quadratis truncatis basi connatis ovariis vix dimidio aequantibus; folliculis maturis ignotis.—ECUADOR: vicinity of Tablon de Oña, Sept. 27, 1918. *J. N. Rose, A. Pachano & G. Rose 23029* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Without any particularly manifest affinities. Although details of the reproductive apparatus undoubtedly prove the species coherent with the other South American species of *Eumandevilla*, the proportions of the corolla are reminiscent of those of *M. convolvulacea* (A. DC.) Hemsl. of southern Mexico.

Mandevilla glandulosa (R. & P.) Woodson, n. comb.

Echites glandulosa R. & P. Fl. Peruv. **2**: 19. *pl. 135*. 1799.

Prestonia Peruviana Spreng. Syst. **1**: 637. 1825.

Haemadictyon glandulosum (R. & P.) A. DC. in DC. Prodr. **8**: 427. 1844.

Odontadenia glandulosa (R. & P.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**^{2}: 169. 1895.

As far as may be ascertained, the original specimen of *Echites glandulosa* collected by Pavon does not exist. The species was unknown both to A. de Candolle and to Miers except as represented in the excellent illustration accompanying Ruiz's description. Consequently its generic status has been somewhat uncertain.

Recently, Weberbauer (no. *4384* in Hb. Berol.) has encountered in flower, as has also Macbride (no. *3730* in Hb. Field Museum) in fruit, a plant almost precisely similar to that illustrated by Ruiz, and for the first time direct evidence may be utilized in interpreting the vexatious question concerning its generic affinity. K. Schumann was impressed by the fact that the five hypogynous nectaries of Weberbauer's specimen are somewhat concrescent and that the inflorescence is opposite, and thus concluded that it should be included within *Odontadenia* Benth., overlooking the glandular emergences at the base of the midrib upon the ventral surface of the foliage, the obscurely auriculate anthers, and the pentagonal-umbraculiform stigma, which necessitate its inclusion within *Mandevilla* Lindl. subgen. *Eumandevilla*.

The only feature which the species in question does not have in common with the other known species of *Mandevilla* is the opposite disposition of the axillary racemes. That phenomenon should not be regarded as of great importance, however, as the characteristic alternate branching has been observed to become opposite in cases of previous injury, and in many instances dormant or abortive branch buds may be observed opposite the functional branch or inflorescence. Furthermore, opposite branching has been found normally at the lower nodes of virtually all species, and may logically be viewed as a primitive structural feature.

Mandevilla Bridgesii (Muell.-Arg.) Woodson, n. comb.

Amblyanthera Bridgesii Muell.-Arg. Linnaea **30**: 420. 1860.

Mandevilla Mandoni Britton, Bull. Torrey Bot. Club **25**: 496. 1898.

Mandevilla Bangii Rusby, Bull. N. Y. Bot. Gard. **4**: 315. 1907.

A species much collected in Bolivia in recent years. Most closely related to the following:

Mandevilla laxa (R. & P.) Woodson, n. comb.

Echites laxa R. & P. Fl. Peruv. **2**: 19. *pl. 134*. 1799.

Mandevilla suaveolens Lindl. Bot. Reg. **3**: 7. *pl. 7*. 1840.

Echites suaveolens (Lindl.) A. DC. in DC. Prodr. **8**: 452. 1844, not Mart. & Gal.

Amblyanthera suaveolens (Lindl.) Muell.-Arg. Linnaea **30**: 447. 1860.

Mandevilla Tweediana Gadeceau & Stapf, Bull. Soc. Sci. Ouest Fr. III. **3**: 2. 1913.

Although it has been impossible to locate an authentic specimen of Ruiz's species, there can be little doubt that his illustration and that of Lindley, accompanied in the latter instance by an indubitable description of the familiar plant of horticulture, are essentially conspecific. Unfortunately, *M. suaveolens*, which is displaced by the earlier name, is the type of the genus *Mandevilla* Lindl.

Mandevilla grata Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracillimis juventate minute puberulo-papillatis tandem glabratis; foliis oppositis longiuscule petiolatis membranaceis ovato-cordatis apice breviter acuteque acuminatis 7–12 cm. longis 5–9 cm. latis supra juventate minute puberulo-papillatis mox glabratis nervo medio basi pauciglanduliferis subtus vix pallidioribus praecipue in nervis venisque laxe villosulis; petiolis 2.0–3.5 cm. longis glabratis; inflorescentiis racemosis lateralibus alternatis folia vix duplo superantibus 4–12-floris; pedunculo parte circa dimidio inferiore sterili deinde laxe florifero glabro; pedicellis 1.5–2.0 cm. longis; bracteis lanceolatis acuminatis 0.5–1.0 cm. longis subfoliaceis; calycis laciniis oblongo-linearibus acuminatis 1 cm. longis subfoliaceis extus glabris intus basi in marginibus squamellas 3–5 denticulatas gerentibus; corollae (ut videtur albae dilute flavescentis) infundibuliformis tubo proprio cylindrico breviusculo 1 cm. longo basi ca. 0.3 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus tubuloso-conicis tubo proprio aequantibus vel eum paulo superantibus ostio ca. 0.4–0.5 cm. diametro metiente lobis inaequilateraliter ovatis vix dolabriformibus 0.5–0.7 cm. longis patulis; antheris anguste oblongis basi obsolete truncateque auriculatis 0.8–0.9 cm. longis; ovariis oblongoideis ca. 0.2 cm. longis apice in stylo

crassiusculo gradatim attenuatis glabris; stigmate proprio 0.3 cm. longo apiculis inconspicuis; nectarii glandulis ovoideo-reniformibus truncatis plus minusve connatis ovariis dimidio vix aequantibus; folliculis ignotis.—ARGENTINA: Tucuman: Muñecas, March 5, 1923. *S. Venturi 1769a* (Mo. Bot. Garden Herbarium, TYPE).

M. grata finds its closest affinity with the Bolivian *M. Bridgesii*. It is distinct by reason of practically every dimension of the corolla, which is much smaller in general, with proportionally longer proper tube and conspicuously shorter lobes of a different shape and position. The pubescence of the foliage, also, although of the same nature as that of the latter species as distinguished from that of the closely neighboring *M. laxa*, is very much sparser and finer, being scarcely perceptible to the unaided eye. The general shape of the leaves, as well as their venation, together with the long, subfoliaceous calyx-lobes and subtubular corolla, serves to impress one with the congenericity of *Mandevilla* Lindl. and the Candollean *Laseguea*.

Mandevilla albo-viridis (Rusby) Woodson, n. comb.

Dipladenia alba-viridis Rusby, Descr. So. Am. Pl. 86. 1920.

There can be little doubt that this plant is congeneric with such species as *M. grata*, *M. Bridgesii*, *M. glandulosa*, and *M. laxa*. The inflorescence of the single specimen constituting the type (*H. H. Smith 1904* in Hb. N. Y. Bot. Garden) is too depauperate to permit thorough examination of the nectaries, which form the sole and all too frequently untrustworthy distinction between *Mandevilla* Lindl. and *Dipladenia* A. DC., but a re-examination of the original dissection, fortunately preserved, discloses that a slip of the needle must have caused an untoward amputation of three of five normal, hypogynous nectaries, thereupon transforming the flower to that of a *Dipladenia!* The occurrence of *M. albo-viridis* in northern Colombia is a considerably boreal extension of the distribution of the typical section of *Eumandevilla*, heretofore confined to Bolivia and adjacent Peru and Argentina.

Mandevilla subsagittata (R. & P.) Woodson, n. comb.

Echites subsagittata R. & P. Fl. Peruv. **2**: 19. 1799.

Echites mucronata R. & S. Syst. **4**: 796. 1819.

Echites Guayaquilensis Benth. Pl. Hartw. 119. 1839.
Echites microcalyx A. DC. in DC. Prodr. **8**: 456. 1844.
Amblyanthera microcalyx (A. DC.) Muell.-Arg. Linnaea **30**: 425. 1860.

This extremely variable and abundant species of Central and northern South America is represented here by only a few of the more familiar names which must be ascribed to it as synonyms. Mueller-Argoviensis was quite aware of the affinities of *E. microcalyx*, which he transferred to his invalid genus *Amblyanthera*, noting in the case of the earlier *E. subsagittata* "*est Amblyantherae spec. forte ab A. microcalyce non diversa*" (loc. cit. 453. 1860). A specimen collected by Pavon at Guayaquil and at present deposited in the Herbier Boissier should probably be considered as authentic.

Mandevilla villosa (Miers) Woodson, n. comb.
Laseguea villosa Miers, Apoc. So. Am. 250. 1878.
Echites comosa O. Ktze. Rev. Gen. **2**: 414. 1891.

Differing from *M. subsagittata* chiefly in the conspicuous, foliaceous, or petaloid bracts, and for that reason placed within the genus *Laseguea* by Miers.

Mandevilla Fendleri (Muell.-Arg.) Woodson, n. comb.
Amblyanthera Fendleri Muell.-Arg. Linnaea **30**: 417. 1860.

The publication of this species under the pre-empted and antedated name *Amblyanthera* requires a recombination under *Mandevilla*, as also is the case of the immediately following:

Mandevilla Schlimii (Muell.-Arg.) Woodson, n. comb.
Amblyanthera Schlimii Muell.-Arg. Linnaea **30**: 419. 1860.

Mandevilla symphitocarpa (G. F. W. Mey.) Woodson, n. comb.
Echites symphitocarpa G. F. W. Mey. Prim. Fl. Esseq. 132. 1818.

Differs from *M. scabra* (R. & S.) K. Sch. chiefly in the generally larger floral organs and in the lack of a vegetative indument. Apparently confined to Trinidad and the Guianas.

Mandevilla Trianae Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus gracillimis molliter puberulo-hirtellis rarius

glabratis; foliis oppositis breviter petiolatis membranaceis late ovato-lanceolatis apice acutiusculis basi gradatim rotundatis et obsolete cordatis plerisque 6–12 cm. longis 2–4 cm. latis supra minute puberulis glabratisve nervo medio in longitudinem pluriglandulosis subtus puberulis; petiolis 0.3–0.6 cm. longis ut in folio vestitis; inflorescentiis racemosis lateralibus alternatis; pedunculo puberulo folia vix superante 6–10-florifero; pedicellis laxis 0.4–0.6 cm. longis; calycis laciniis lanceolatis acuminatis 0.1–0.2 cm. longis extus minute puberulis intus basi squamellam parvam deltoideam minute denticulatam gerentibus; corollae infundibuliformis tubo proprio breviuscule cylindrico 1.75–2.0 cm. longo basi ca. 0.1 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus conico-cylindricis 1.5–1.75 cm. longis ostio ca. 0.75 cm. diametro metiente lobis oblique obovatis acutiusculis faucibus vix aequantibus evidenter plus minusve patentibus; antheris anguste elliptico-oblongis basi obscure auriculatis 0.4 cm. longis; ovariis oblongoideis 0.15 cm. longis apice plus minusve gradatim attenuatis minute puberulis; stigmate proprio ca. 0.2 cm. longo apicula terminalia quadruplo superante; nectarii glandulis oblongo-ovoideis distinctis ovariis ca. dimidio brevioribus; folliculis ignotis.—COLOMBIA: Choco: "alt. 150 m., April, 1853." *J. J. Triana 3409* (Herbarium British Museum, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Evidently allied to *M. Schlimii* because of the tubular or cylindrical corolla-throat, but differing in the larger leaves of a distinct shape, as well as in the dimensions of the flowers. It appears to be a species limited to the northern Pacific Coastal Zone of South America, having been collected by Pittier (no. *520* in U. S. Nat. Hb.) in the state of Cauca, Colombia, and by Andrè (no. *3590* in Hb. Kew.) upon the western slope of the Ecuadorian Andes.

Mandevilla subpaniculata Woodson, n. name

Echites macrophylla A. Zahlbr. Ann. K.K. Naturh. Hofmus. Wien **7**: 5. 1892, not HBK.

The most striking feature displayed by this species is the complete lack of the usual nectaries surrounding the ovary. In view of the great variability of this character in both *Mandevilla* Lindl.

and *Dipladenia* A. DC., it has been considered advisable to refer the species to the former rather than to establish a new genus for its inclusion.

Mandevilla sagittarii Woodson, sp. nov., suffruticosa volubilis; ramulis teretibus crassiusculis sparse ferrugineo-hispidulis; foliis oppositis longiuscule petiolatis membranaceis late oblongo-ellipticis apice abrupte acuminatis acute subcaudatis basi gradatim attenuatis et obscure cordatis 8–12 cm. longis 4–6 cm. latis supra sparse strigillosis nervo medio in longitudinem pluriglandulosis subtus dense tomentulosis; petiolis 1.5 cm. longis dense pilosulis; inflorescentiis racemosis lateralibus alternatis; pedunculo minute hispidulo 5–15-florifero foliis fere dimidio aequante; pedicellis 0.75 cm. longis post maturitatem parum accrescentibus; bracteis magnis ovatis caudato-acuminatis sessilibus 1.0–1.5 cm. longis laxe pilosulis rubidulo-coloratis; calycis laciniis linearo-lanceolatis acuminatis 0.75 cm. longis extus sparse minuteque pilosulis intus basi squamellam deltoideam apice indistincte denticulatam gerentibus; corollae infundibuliformis (ut dicitur dilute flavidulae) extus pilosulae tubo proprio longiuscule cylindrico paulo ventricoso 2.5 cm. longo basi ca. 0.2 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus late tubulosis paulo inaequilateralibus 3 cm. longis ostio ca. 0.75 cm. diametro metiente lobis oblique lateque obovatis 1.5 cm. longis valde patentibus; antheris oblongo-ellipticis basi anguste obsoleteque auriculatis 0.35 cm. longis; ovariis ovoideis 0.2 cm. longis apice in stylo gracili gradatim angustatis glabris vel minutissime papillatis; stigmate proprio ca. 0.15 cm. longo apicula sterilia ter superante; nectarii glandulis subquadratis basi connatis ovariis dimidio aequantibus; folliculis obscure moniliformibus 12–15 cm. longis plus minusve falcatis hispidulo-strigillosis; seminibus subscaphiformibus 1 cm. longis como 2 cm. longo aurantiaco.—COLOMBIA: Choco: between La Oveja and Quibdo, April 1–2, 1931. *W. A. Archer 1714* (U. S. National Herbarium, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

Without doubt closely related to *M. hirsuta* (A. Rich.) K. Sch., but differing markedly in the tubular corolla-throat which strongly resembles that of an *Odontadenia*.

Mandevilla Pavonii (A. DC.) Woodson, n. comb.

Echites hirsuta R. & P. Fl. Peruv. **2**: 19. *pl. 136.* 1799, not A. Rich.

Prestonia hirsuta (R. & P.) Spreng. Syst. **1**: 637. 1825.

Echites Pavonii A. DC. in DC. Prodr. **8**: 463. 1844.

The writer has been unable to locate Pavon's original specimen in the Herbier Boissier as indicated by de Candolle, but feels confident in making the above recombination upon the basis of the original illustration which agrees essentially with two collections recently made in eastern Peru by G. Klug (nos. *1288* & *57* in U. S. Nat. Hb.).

Mandevilla bogotensis (HBK.) Woodson, n. comb.

Echites Bogotensis HBK. Nov. Gen. **3**: 215. *pl. 243.* 1818.

Amblyanthera Bogotensis (HBK.) Muell.-Arg. Linnaea **30**: 452. 1860.

Anartia Bogotensis (HBK.) Miers, Apoc. So. Am. 82. 1878.

As in *M. subpaniculata*, the nectaries of this species are obsolete. In spite of this anomaly, however, Mueller was fully aware of the generic affinities of the plants, transferring them to his invalid genus *Amblyanthera*. The absence of the gynoecial nectaries, usually prominent features of the American species of Echitoideae, is presumably responsible alone for Miers's transfer of the species to *Anartia* Miers, a dubious segregate of the inclusive genus *Tabernaemontana* L.

Mandevilla polyantha K. Sch. in herb., suffruticosa volubilis; ramulis teretibus gracillimis pilosis; foliis oppositis longiuscule petiolatis membranaceis late ellipticis acuminatis obscure angusteque cordatis 7–12 cm. longis 3–6 cm. latis supra nitidulis nervo medio in longitudinem pilosulis et pluriglandulosis subtus pallidioribus praecipue in nervis venisque laxe puberulis; petiolis 1.0–1.5 cm. longis ut in ramulis vestitis; inflorescentiis racemosis lateralibus alternatis; pedunculo glaberrimo 20–35-florifero folia vix duplo superante; pedicellis subsecundis 1 cm. longis post maturitatem longe accrescentibus; bracteis linearibus scariaceis minimis; calycis laciniis late trigonalibus acutiusculis 0.1 cm. longis scariaceis extus dense puberulo-papillatis intus basi squa-

mellam deltoideam denticulatam gerentibus; corollae (viridoflavidulae ?) infundibuliformis extus glabrae tubo cylindrico ventricoso 1.0–1.25 cm. longo basi ca. 0.15 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus conicis parum inaequilateralibus 1 cm. longis ostio ca. 0.5 cm. diametro metiente lobis oblique obovato-reniformibus 0.25 cm. longis valde patentibus; antheris cuneato-ellipticis basi angustissime auriculatis 0.3 cm. longis; ovariis oblongo-ovoideis 0.15 cm. longis omnino glabris; stigmate proprio 0.1 cm. longo apicula terminalia ca. ter superante; nectarii glandulis ovoideo-dentiformibus basi plus minusve connatis ovariis vix aequantibus; folliculis maturis ignotis.—PERU: Loreto: Yurimaguas, Aug., 1902. *E. Ule 6271* (Herbarium Bot. Gart. Berlin-Dahlem, TYPE, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

This interesting species, which more recently has been collected by Killip & Smith (no. *27579* in U. S. Nat. Hb.) in the same general locality as that of the type specimen, recalls to a certain extent the aspect of *M. Moritziana* of Venezuela, but differs in the smaller, more gibbous corolla, the inconspicuous, scarious bracts, and the indument of the vegetative parts. The species was noted as a *nomen nudum* in Engl. Bot. Jahrb. **40**: 403. 1908.

Mandevilla lancifolia Woodson, sp. nov., suffruticosa erecta altitudine ignota; ramis subteretibus vel plus minusve alatis juventate dense puberulo-papillatis tandem glabratis cortice griseo-brunneis; foliis oppositis brevissime petiolatis rigide membranaceis anguste linearo-lanceolatis 3–6 cm. longis 0.5–0.75 cm. latis omnino glabris nervo medio ventro in longitudinem inconspicue pauciglanduligero; petiolis 0.1–0.2 cm. longis glabris; inflorescentiis racemosis lateralibus alternatis; pedunculo glabro 1–7-floro foliis dimidio aequante; pedicellis 0.15 cm. longis; bracteis ovatis scariaceis minimis; calycis laciniis ovatis acutiusculis 0.15–0.2 cm. longis scariaceis extus glabris vel minutissime papillatis intus basi squamellam deltoideam profunde laciniatam gerentibus; corollae (ut videtur rubidulo-flavidulae) infundibuliformis tubo proprio gracile cylindrico 1 cm. longo basi ca. 0.1 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus tubulo-conicis 1.5–2.0 cm. longis ostio ca. 0.5 cm. diametro

metiente lobis oblique obovatis obtusiusculis 1.5–2.0 cm. longis patulis; antheris oblongis basi obscure truncateque auriculatis 0.6 cm. longis; ovariis anguste oblongoideis apice in stylo capillaceo gradatim angustatis 0.2 cm. longis omnino glabris; stigmate proprio 0.2 cm. longo apiculis terminalibus vix manifestis; nectarii glandulis ovoideo-quadratis basi connatis ovariis quadruplo brevioribus; folliculis linearo-cylindricis acuminatis obscure articulatis laevibus 7–10 cm. longis; seminibus subscaphiformibus 0.5 cm. longis como 1.5 cm. longo aurantiaco.—VENEZUELA: Amazonas: Puerto Ayacucho: alt. 100 m., May, 1931. *E. G. Holt & E. R. Blake 780* (Mo. Bot. Garden Herbarium, TYPE, U. S. National Herbarium, duplicate).

A very distinct and showy species, conspicuous because of its dense, narrow foliage, and bright flowers, which was collected in 1854 by Richard Spruce (no. *3610* Hbb. Kew. & Vindob.) in approximately the same general locality on the upper Orinoco. *M. lancifolia* constitutes a rather unique addition to *Mandevilla* sect. *Eriadenia* Mgf., and appears to have no very definite affinities. From *M. Benthamii* (A. DC.) K. Sch., which it simulates very generally because of its narrow foliage, it may be distinguished by means of the opposite phyllotaxy and the narrower corolla-throat. *M. lancifolia* would also appear to attain a greater height than does the latter species.

Mandevilla anceps Woodson, sp. nov., suffruticosa erecta; ramulis crassiusculis distincte ancipibus juventate dense minuteque puberulis tandem glabratis; foliis oppositis breviuscule petiolatis subcoriaceis late elliptico-oblongis obsolete cordatis apice obtusiusculis 5–8 cm. longis 2–3 cm. latis supra minute puberulo-papillatis mox glabratis nervo medio in longitudinem inconspicue pauciglanduligero subtus pallidioribus dense puberulis; petiolo 0.5 cm. longo minute puberulo; inflorescentiis racemosis lateralibus alternatis; pedunculo 3–5-floro petiolos paulo superante; pedicellis 0.2–0.3 cm. longis; bracteis ovatis scariaceis minimis; calycis laciniis ovato-lanceolatis acuminatis 0.15 cm. longis scariaceis extus minute puberulo-papillatis intus basi squamellam deltoideam laciniatam gerentibus; corollae (flavidulae ?) infundibuliformis extus minute puberulae tubo proprio anguste cy-

lindrico 2.5–3.0 cm. longo basi ca. 0.1 cm. diametro metiente ad apicem staminigero ibique dilatato faucibus conicis 2 cm. longis ostio ca. 1 cm. diametro metiente lobis oblique obovato-reniformibus 1.5 cm. longis valde patentibus; antheris anguste oblongis basi truncate auriculatis 0.5 cm. longis; ovariis oblongo-ovoideis apice abrupte angustatis ca. 0.1 cm. longis dense puberulo-papillatis; stigmate proprio 0.15 cm. longo apiculis sterilibus terminalibus vix manifestis; nectarii glandulis oblongoideis basi connatis ovariis vix aequantibus; folliculis anguste teretibus paulo articulatis 9 cm. longis minute puberulis; seminibus subscaphiformibus 0.5 cm. longis como 1.5 cm. longo aurantiaco.—Brazil: "in montic. Tarurumari fluvii Pacimoni, Feb., 1854." *R. Spruce 3395* (Herbarium Kew., type, Mo. Bot. Garden Herbarium, photograph and analytical drawings).

In *M. anceps*, the predominantly alate stems of *Mandevilla* sect. *Eriadenia* Mgf. attain their greatest development. The species is also noteworthy as being the only known member of the section with a well-developed vegetative indument.

A NEW SCAPOSE DRABA FROM UTAH

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Among the plants collected by the authors in the southwestern United States during the summer of 1930 is a *Draba* which, upon further study, seems to warrant specific recognition. It is described as follows:

Draba subalpina[1] Goodman and Hitchcock, n. sp. Caespitose perennial, the leaves forming rosettes; leaves linear-oblanceolate, entire, obtuse, 6–11 mm. long, midvein apparent, glabrous except for the setose-ciliate simple hairs on the margins; scapes solitary or few, glabrous, 4–6 cm. tall; fruiting inflorescence a lax raceme; pedicels ascending, 4–8 mm. long; siliques ovate to oblong-ovate, flattened, glabrous, 4–7 mm. long, 3–3.5 mm. broad, style 0.7 mm. long; ovary 6–8-ovuled; flowers unknown.—Utah: meadowland, Cedar Breaks, 3,000 m. alt., July 18, 1930, *Goodman & Hitchcock 1622* (Mo. Bot. Gard. Herb., TYPE); Cedar Breaks, July 17, 1922, *M. E. Jones* (Pomona Coll. Herb. No. 117158).

The nearest relative of this species probably is *Draba oreibata* Macbride & Payson, the type of which was collected in central Idaho. *D. subalpina* differs from Macbride and Payson's plant in the larger leaves and in the broader, ovate instead of elliptic siliques. A technical and anatomical difference between the two

[1] **Draba subalpina** Goodman et Hitchcock, sp. nov. Planta perennans caespitosa; foliis 6–11 mm. longis, rosulatis lineari-oblanceolatis, obtusis, integris, utrinque glabris, marginibus setoso-ciliatis, pilis simplicibus; scapis fructiferis 4–6 cm. altis, glabris, solitariis vel paucis; racemis laxis; pedicellis 4–8 mm. longis, ascendentibus; siliquis 4–7 mm. longis, 3–3.5 mm. latis, ovatis vel oblongo-ovatis, compressis, glabris, stylo 0.7 mm. longo; ovario 6–8-ovulato; floribus non visis.—Utah: meadowland, Cedar Breaks, 3,000 m. alt., July 18, 1930, *Goodman & Hitchcock 1622* (Mo. Bot. Gard. Herb., TYPE); Cedar Breaks, July 17, 1922, *M. E. Jones* (Pomona Coll. Herb. No. 117158).

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species is to be found in the outline of the cells of the septum. In *D. oreibata*, as well as in *D. cyclomorpha* and *D. Lemmonii*, these cells are relatively small and in the first mentioned are irregular in outline, more or less straight-sided, and not more than twice so long as broad. In *D. subalpina* the cells of the septum are large, deeply tortuous in outline, and more than three times as long as broad.

Goodman and Hitchcock's No. 1622 was distributed as "*Draba Lemmonii* Wats." under which name it may be found in herbaria.

THE INJURIOUS EFFECTS OF ULTRA-VIOLET AND INFRA-RED RADIATIONS ON PLANTS

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1. Previous Work

Numerous investigations have demonstrated that the radiations emanating from unscreened carbon and quartz-mercury-vapor arcs are decidedly injurious to plant tissue. These effects are quite striking: leaves are glazed and bronzed, the upper epidermis is burned off, stems made brittle, growth stunted. The manifestations of injury have in general been attributed to the ultra-violet wave lengths generated by the arcs; possible effects of the infra-red portion of the spectrum have been almost entirely neglected, not only in the earlier works, but as late as 1929.

Delf, Ritson, and Westbrook ('27) rayed seedlings of *Arachis* and *Trifolium* at 24 inches from a mercury arc and reported injuries which they attributed to ultra-violet. Popp and Brown ('28) rayed cucumbers, turnip, and other species of plants at a distance of 50 cm.—only 20 inches—from an unscreened mercury vapor arc and found that "ultra-violet radiation caused only injury to all the seedlings used." Newell and Arthur ('29) rayed tomato plants at 15 inches with the full spectrum of the mercury vapor arc and wrote of the injurious effects induced by "ultra-violet radiation." It seems incredible that the injury produced in plants when they are irradiated at such short distances from the arc is attributable exclusively to ultra-violet radiation. Intensity measurements made in this laboratory show that at such close proximity to the arc, the infra-red radiation may constitute as much as 90 per cent of the total energy output of the arc. In view of this condition it seems that the infra-red radiation might account for a considerable part of the injury usually referred to the ultra-violet portion of the spec-

trum. The experiments herein reported attempted to determine whether or not this assumption is valid—that is, to what degree the infra-red radiation is responsible for injury to plant tissue.

II. EXPERIMENTAL

The plants used in these experiments were "Bonny Best" tomatoes and red kidney field beans. Plants were grown individually in pots, and at the beginning of irradiation the tomatoes averaged about 7.0 cm. in height, the beans about 21.0 cm. Three experimental groups of both species were arranged as follows:

A. Controls—not rayed.

B. Exposed to a Burdick Quartz Mercury-Vapor arc screened by a quartz cell containing 1.5 cm. of distilled water which provided ultra-violet transmission to 210 mμ but which removed the greater part of the infra-red portion of the spectrum (Luckiesh, '27, pp. 49–50).

C. Exposed to the full spectrum of a Burdick Mercury-Vapor arc transmitting to 210 mμ.

The ultra-violet output of the arc was measured by a Burt ultra-violet photometer; at a distance of 40 cm. from the arc, the ultra-violet intensity per square centimeter of receptive surface was 54 Burt ultra-violet units (grams-calories per square centimeter per minute). The same readings were obtained with the unscreened arc and with the quartz-water cell before the arc; that is, the 1.5-cm. water layer caused no diminution in the intensity of the ultra-violet transmitted. Spectrographs showed also a similar qualitative transmission with and without the quartz-water cell.

Twelve plants of each species were used in each group, with the intention of increasing the numbers later. The results were so conclusive, however, as to exclude errors contributed by individual variation among the plants. The plants were rayed at 15 inches—38 cm.—from the arc for nine days for three minutes daily, during which time significant changes were observed and measurements of increase in height and leaf number were made.

III. Results

1. Tomatoes.—The first signs of injury appeared in the tomatoes 24 hours after the first irradiation, in group C. The epidermal hairs were burned off and a few shiny areas were present on the uppermost leaves of the plants. These signs of injury became intensified with succeeding exposure periods. At the end of nine days the leaves were bronzed and quite brittle, growth had ceased completely, and the plants were obviously dying.

Group B showed definite injury, however to a lesser degree than did group C. In B, the first signs of glazing of leaves appeared after the fourth daily irradiation, a condition comparable to that of C after its first irradiation. At the end of the nine-day period, the total injury in group B consisted of a general glazing of the upper leaves, with a few small bronzed patches scattered here and there; the plants were somewhat stunted in growth but were still growing. They showed considerably less injury than did group C.

Growth measurements of the tomatoes appear in table 1:

TABLE I.—TOMATOES

Plant Number	Beginning of irradiation		End of irradiation		Increase in height (cm.)	Increase in number of leaves
	Height in cm.	Number of leaves	Height in cm.	Number of leaves		
Group A: Controls						
1	6.5	6	14.5	8	8.0	2
2	7.0	6	14.0	7	7.0	1
3	7.0	5	15.5	7	8.5	2
4	6.0	5	14.4	7	8.4	2
5	6.5	6	15.1	7	8.6	1
6	8.5	6	17.6	7	7.1	1
7	7.3	7	15.6	8	8.3	1
8	7.7	6	15.0	8	7.3	2
9	6.7	5	14.3	7	7.6	2
10	6.2	5	13.1	6	6.9	1
11	7.1	6	14.6	7	7.5	1
12	6.8	6	15.0	7	8.2	1
				Average	7.78	1.41

Group B: Quartz-water cell

1	7.0	5	12.8	7	5.8	2
2	6.0	5	13.1	7	7.1	2
3	7.0	6	13.0	6	6.0	0
4	6.2	5	13.2	6	7.0	1
5	7.0	6	13.0	8	6.0	2
6	7.5	6	13.6	8	6.1	2
7	6.1	6	12.5	7	6.4	1
8	7.3	7	13.5	7	5.8	0
9	7.1	6	14.0	7	6.9	1
10	6.7	5	12.7	7	6.0	2
11	6.1	5	11.9	6	5.8	1
12	6.4	6	12.7	8	6.3	2
				Average	6.33	1.33

Group C: Open arc

1	7.0	6	11.5	6	4.5	0
2	8.0	6	13.2	7	5.2	1
3	6.5	5	11.5	6	5.0	1
4	7.7	5	13.0	5	5.3	0
5	7.5	6	11.5	6	4.0	0
6	9.0	6	13.5	7	4.5	1
7	7.6	6	11.3	7	3.7	1
8	8.2	6	11.5	6	3.3	0
9	8.4	5	11.9	5	3.5	0
10	7.7	5	11.1	6	3.4	1
11	8.1	6	Dead			
12	6.9	5	10.7	6	3.8	1
				Average	4.20	0.54

2. Beans.—The first signs of injury appeared within 20 hours after the first irradiation period, in group C, as a glazing of the upper leaves. In group B, the leaves showed a comparable condition after the third irradiation period. The plants in group C after the second raying tended to wilt, and the uppermost leaves appeared more or less scorched and dried; the lower leaves soon became bronzed and curled after three or four periods of irradiation. The results in general were quite comparable with those obtaining in the tomatoes: the plants in group C in the beans were near death at the end of nine days, whereas those in B were still growing, although they did show definite signs of injury. The beans seemed more sensitive for the most part to the irradiations than did the tomatoes. The measurements of the beans are presented in table II.

TABLE II.—BEANS

Plant Number	Beginning of irradiation		End of irradiation		Increase in height (cm.)	Increase in number of leaves
	Height in cm.	Number of leaves	Height in cm.	Number of leaves		
Group A: Controls						
1	20.5	1	32.5	6	12.0	5
2	23.5	1	38.0	6	14.5	5
3	24.0	1	38.5	6	14.5	5
4	20.0	1	36.0	6	16.0	5
5	23.0	1	36.5	6	13.5	5
6	21.0	1	35.0	6	14.0	5
7	21.0	1	40.0	7	19.0	6
8	22.5	1	38.5	6	16.5	5
9	24.0	1	Dead			
10	21.5	1	37.5	6	16.0	5
11	18.0	1	29.0	6	11.0	5
12	23.0	1	43.0	7	20.0	6
				Average	15.09	5.18
Group B: Quartz-water cell						
1	23.0	1	32.5	5	9.5	4
2	24.5	1	34.5	5	10.0	4
3	22.5	1	32.0	5	9.5	4
4	21.5	1	30.0	5	7.5	4
5	24.0	1	35.0	5	11.0	4
6	21.0	1	29.5	4	8.5	3
7	24.0	1	Dead			
8	21.0	1	28.5	4	7.5	3
9	24.0	1	35.0	5	11.0	4
10	26.0	1	34.5	4	7.5	3
11	26.0	1	37.0	5	11.0	4
12	20.5	1	33.5	5	13.0	4
				Average	9.63	3.45
Group C: Open arc						
1	20.5	1	24.0	3	3.5	2
2	18.0	1	20.0	4	2.0	3
3	21.0	1	25.0	3	4.0	2
4	24.0	1	28.0	3	4.0	2
5	25.0	1	28.0	3	3.0	2
6	23.0	1	29.0	3	6.0	2
7	22.5	1	27.0	3	4.5	2
8	20.5	1	26.0	3	6.0	2
9	23.5	1	27.0	3	3.5	2
10	24.0	1	29.0	4	5.0	3
11	25.0	1	28.0	3	3.0	2
12	22.0	1	27.5	3	5.5	2
				Average	4.16	2.25

Photographs of the beans and tomatoes are included in plate 3; the plants selected for photographs were some which were nearest the group average in each case.

IV. Summary

1. Radiations from an unscreened quartz mercury vapor arc produce decided injury in the tissues of tomato and bean plants at 15 inches from the arc; in addition, growth rate and leaf production are repressed.

2. The injurious effects at this distance are due in considerable degree to infra-red radiation from the arc.

3. The injurious effects are considerably reduced when a quartz water cell, which screens out infra-red radiation, is interposed between the arc and the plants.

4. It should be emphasized that the present work does not involve problems of stimulation, as previously reported; under the conditions used in this present experimentation, only injurious effects were observed. Stimulatory effects of ultra-violet radiation occur under markedly different methods of treatment, as previously employed.

V. Acknowledgments

The author expresses his gratitude to Dr. Ernest S. Reynolds, under whose general supervision a series of experiments on ultra-violet radiation is being carried out.

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Explanation of Plate

PLATE 3

Fig. 1. Beans.
A—Control.
B—Quartz-water cell.
C—Open arc.

Figs. 2–3. Tomatoes.
A—Control.
B—Quartz-water cell.
C—Open arc.

1

2

3

FULLER—EFFECTS OF ULTRA-VIOLET AND INFRA-RED RADIATIONS

A REVISION OF THE GENUS MENODORA[1]

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History

The genus *Menodora* was founded in 1809 by Humboldt and Bonpland[2] in the 'Plantes Aequinoxiales'; it was based on a Mexican plant, collected on their expedition to Mexico, Central and South America, which was described and illustrated as *Menodora helianthemoides*. The word *Menodora*, derived from the Greek words, μένος, force or courage, and δῶρον, gift, had reference to the force or strength it gave to animals. Since the fruit was unknown to them, Humboldt and Bonpland doubtfully referred the genus to the natural family Jasmineae (now Oleaceae), as established by Jussieu[3] in his 'Genera Plantarum.' In 1825 Kunth[4] elaborated upon the original description of this new genus, making use of the type material. Unfortunately, these specimens had no fruit and thus his description of the fruit as a bilocular, bivalved capsule was taken solely on the faith of Bonpland. He added one significant character, namely, that there were two ovules in each of the two cells of the ovary; he assigned *Menodora* to the Acanthaceae.

The following year Chamisso and Schlechtendal[5] in 'Linnaea' published a new genus, called *Bolivaria*, in honor of Simon Bolivar, the liberator of South America. The plants were collected in the vicinity of Buenos Aires, Argentina, and described as two species, *B. integrifolia* and *B. trifida*. The striking features of these South American plants were their circumscissile capsules, 5-parted calyx, and 4-seeded cells of the fruit; these characters were considered to be generically distinct from the multifid calyx,

[1] A dissertation presented to the Board of Graduate Studies of Washington University in partial fulfilment of the requirements for the degree of Master of Science.

[2] Humboldt, A. & Bonpland, A. Pl. Aequin. **2**: 98. *pl. 110.* 1809.

[3] Jussieu, A. L. Gen. Pl. 104. 1789.

[4] Kunth, C. S., in HBK. Nov. Gen. et Sp. Pl. **7**: 199. 1825.

[5] Chamisso, A. & Schlechtendal, D., in Linnaea **1**: 268, *pl. 4, fig. 1.* 1826.

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bi-ovulate cells of the ovary, and supposedly bivalved capsule of *Menodora*, and thus *Bolivaria* was treated as a new genus, being placed in the Gentianeae.

Bartling[6] recognized both *Menodora* and *Bolivaria* as distinct genera in his 'Ordinales Naturales Plantarum' in 1830, but was in doubt as to their affinities with other genera. He grouped them with other monopetalous genera under the heading, "Genera Dicotyledonea dubia l. incertae sedis."

Dietrich[7] did not approve of *Bolivaria* as a name for a genus, believing that celebrated men in history and politics should not figure in botanical nomenclature. Therefore, he substituted in 1831 in the 'Species Plantarum' the name *Calyptrospermum* for *Bolivaria*. This generic name, however, did not persist, because of the priority of the name *Bolivaria*.

Another species, *Bolivaria decemfida*, was described by Gillies[8] from a South American plant in 1834 in Hooker's 'Journal of Botany.'

In his 'Natural System of Botany' in 1836 Lindley[9] placed *Bolivaria* under the Jasminaceae, regarding *Menodora* as its synonym. In 1838 G. Don,[10] in 'General History of the Dichlamydeous Plants,' recognized both *Bolivaria* and *Menodora*, and assigned them to the Columellieae in coördinate family rank with Oleineae and Jasminaceae. Grisebach[11] further confused the arrangement of *Menodora* and *Bolivaria* in 1839 in his 'Genera et Species Gentianearum' by creating for these genera a separate family, Bolivariaceae. He considered this family as one showing natural affinity with the Gentianeae.

In 1841 Steudel[12] in his 'Nomenclator Botanicus' transferred *Bolivaria trifida* and *B. integrifolia* to the genus *Menodora*.

Endlicher[13] in 'Enchiridion Botanicum' in 1841 recognized *Menodora* and *Bolivaria* as distinct genera. Doubt was expressed as to the number of seeds in each cell of the capsule.

[6] Bartling, F. J. Ord. Nat. Pl. 427–428. 1830.
[7] Linnaeus, C. Sp. Pl. [A. Dietrich], ed. 6. **1**: 227. 1831.
[8] Gillies, in Hook. Jour. Bot. **1**: 284. 1834.
[9] Lindley, J. Nat. Syst. Bot. ed. 2. 309. 1836.
[10] Don, G. Gen. Hist. Dichl. Pl. **4**: 58. 1838.
[11] Grisebach, A. H. R. Gen. et Sp. Gentian. 20. 1839.
[12] Steudel, E. T. Nom. Bot. ed. 2. **2**: 124. 1841.
[13] Endlicher, S. Ench. Bot. 285. 1841.

In 1842 the fifth species, an African one, and the first to be described from the Old World, *Menodora africana*, was published by Sir Wm. J. Hooker[14] in Hooker's 'Icones Plantarum,' and supplemented with a good illustration.

In the 'Prodromus' in 1844 de Candolle[15] recognized *Menodora* and *Bolivaria* as distinct genera. Two new species were included, *Menodora heterophylla* from Texas and *Bolivaria Mexicana* from Mexico. These two genera were distinguished by the number of seeds in each cell of the capsule, the circumscissile dehiscence of the capsule, and the five to ten calyx-lobes of *Bolivaria*, as contrasted with the supposedly indehiscent capsule, and eleven to fourteen calyx-lobes of *Menodora*.

Between 1846 and 1852 three new species were added to *Bolivaria*, *B. robusta* from Argentina, *B. chlorargantha* from Bolivia, and *B. Grisebachii* from Texas.

In 1852 Asa Gray[16] in the 'American Journal of Science and Arts' showed that *Bolivaria* and *Menodora* were congeneric, and referred all the hitherto-published species of the two groups to *Menodora*, and in addition described four new species, bringing the total known species to thirteen. He recognized three sections in the genus, *Bolivaria*, *Menodora*, and *Menodoropsis*. This treatment of the genus definitely settled the question concerning the retention of *Bolivaria* as a valid genus. In 1878, in his 'Synoptical Flora of North America,' he[17] described all the North American species.

Approximately twenty species and a limited number of varieties have been recorded for the genus *Menodora*, but no comprehensive treatment of the group has been elaborated since de Candolle's 'Prodromus' in 1844.

The writer takes this opportunity to express his appreciation and gratitude to the several persons who have made this study possible. Thanks are due to Dr. George T. Moore, Director of the Missouri Botanical Garden, for the privilege of using the excellent library and herbarium. Especial thanks are due to

[14] Hooker, W. J., in Hook. Ic. Pl. *pl. 586*. 1842.
[15] A. de Candolle, in DC. Prodr. **8**: 315–316. 1844.
[16] A. Gray, in Am. Jour. Sci. II. **14**: 41. 1852.
[17] A. Gray, in Syn. Fl. N. Am. **2**[1]: 78. 1878.

Dr. J. M. Greenman, Curator of the Herbarium of the Missouri Botanical Garden, under whose guidance this revision has been carried on, who at all times lent such helpful aid and criticism. Sincere gratitude is due Dr. Mildred E. Mathias, formerly Research Assistant at the Missouri Botanical Garden, who so kindly gave advice and suggestions. Appreciation is also due the curators of all the herbaria from which material has been borrowed for this study.

GENERAL MORPHOLOGY

The genus *Menodora* presents an interesting habital deviation from the other genera in the Oleaceae, for whereas this family comprises mostly shrubs, trees, or lianas, the genus *Menodora* consists of low suffruticose plants.

Root.—The root system consists of a simple, stout, woody, perennial tap-root, which varies considerably in length. In a few instances in which the plants have been growing on rocky, steep slopes, specimens show the root extending in a horizontal direction. The perennial root develops a thick woody crown, which branches freely, sending out numerous ligneous axes from which the stems of the season develop.

Stem.—The stems present a wide range of conditions. In height they vary from 0.3 to 0.4 dm., as in *M. helianthemoides* var. *Engelmannii* and var. *humilis*, to 11 dm., as in *M. robusta*. The shoots of the coming season develop from the primary ligneous axes. These new stems are subherbaceous in most of the species, as is well shown in *M. heterophylla*, *M. scabra*, and *M. integrifolia* var. *trifida*. In a few cases, however, as in *M. robusta*, *M. spinescens*, *M. juncea*, and others, the suffruticose tendency is more evident.

The stems during the period of growth are simple and elongated, as, for example, in *M. heterophylla* and *M. scabra*, or are markedly branched, as is shown in *M. juncea*, *M. intricata*, *M. decemfida*, and others. The branches are mostly opposite below, but become approximate and then alternate towards the reproductive shoots.

There are two main types of stem habit. In one, which includes the majority of the species, the stems are erect and strict, as in *M. juncea*, *M. scoparia*, *M. robusta*, and *M. longiflora*. In the

other, the stems are more or less decumbent and diffusely spreading, as, for example, in *M. integrifolia* var. *trifida*, *M. helianthemoides* var. *Engelmannii*, *M. helianthemoides* var. *parviflora*, and others. In *M. intricata* they are intricate.

The stems, due to the decurrent petioles, are usually more or less angled. This condition is especially well exemplified in *M. decemfida* var. *longifolia*, *M. intricata*, and *M. scabra*. *Menodora spinescens* and *M. robusta* have terete stems. In *M. intricata* the stems are very much ribbed on account of the decurrent petiole being strongly ridged in the middle and along the margins.

In most of the species the stems are slender, but in *M. robusta* and *M. spinescens* they are stout.

The stems are generally unarmed, but in *M. robusta* a spinescent condition is approximated by the tips of the branches becoming gradually conical. The pseudo-spinosity in *M. robusta* develops into a true spinose state in *M. spinescens* and its variety *mohavensis*.

Leaves.—The leaves are generally opposite, but vary to approximate or alternate as they approach the inflorescence. They may be fascicled, as on some of the flowering shoots of *M. spinescens*. They are mostly sessile, although they may be narrowed at the base into a slight petiole. They are practically always subcoriaceous, and subtended below by a single prominent nerve.

The leaves vary in shape from narrowly linear to suborbicular. They are entire in the majority of the species, but they may be lobed or pinnatifid. In *M. pinnatisecta* they are linear to deeply pinnatisect. This condition becomes even more pronounced in *M. africana*, in which the leaf segments are narrowly linear, less than 0.5 mm. broad, and appear heath-like. The leaves vary in length from 2 to 55 mm., and in breadth from 1 to 30 mm.

A number of species exhibit an interesting reduction series in the foliage. In most species the leaves are foliose throughout. In *M. scabra*, for example, all of the leaves are well developed, and the internodes are short. Beginning with a species, such as *M. scoparia*, the leaves at the base of the branches are foliose and functional, but towards the upper parts of the shoots they show a tendency to become reduced to a more or less rudimentary state, while the internodes become elongated. From such a con-

dition as this it is relatively easy to proceed to a species, such as *M. intricata*, in which all of the leaves have become reduced to a rudimentary state, to *M. juncea* where they have degenerated to mere vestiges, and to *M. robusta*, where, with the exception of a few small leaves on the upper shoots, they are practically obsolete.

Pubescence.—The usual type of pubescence consists of short simple hairs. Frequently the pubescence on the stems is confined to the margins of the decurrent petioles. It may be very sparse, as in *M. heterophylla*, or more pronounced, as in *M. Coulteri*, *M. helianthemoides*, *M. scabra*, and hairy forms of *M. longiflora*. The last species varies from entirely glabrous to densely pubescent. Most of the pubescent species are more or less scabrous. *Menodora scabra* and its varieties, *M. Coulteri*, *M. intricata* var. *Purpusii*, *M. longiflora*, and *M. helianthemoides* var. *magniflora* are examples of species in which the scabrous hairs are scattered and diffusely spreading, whereas *M. helianthemoides* var. *Engelmannii* and *M. spinescens* possess a very short closely appressed type of hirtellous pubescence. *Menodora helianthemoides* and its variety *humilis*, and some extremely pubescent forms of *M. longiflora* are striking instances of species possessing relatively long, spreading hairs of a hirsute-pilose nature. Some of the species of *Menodora*, such as *M. decemfida*, *M. intricata*, *M. juncea*, *M. integrifolia*, and *M. pinnatisecta*, are glabrous throughout.

Inflorescence.—The inflorescence fundamentally is cymose. In all cases it probably has been derived from a dichasium. In *M. scabra* and *M. longiflora* the cyme is many-flowered and subcorymbose, whereas in *M. scoparia* it is more or less paniculate. In *M. pinnatisecta* it is dichasial below, but shows a tendency to become monochasial above. The flowers appear solitary and remote, and terminal or axillary in the upper leafy branches in those species which have a reduced cyme. Such a type occurs in the decumbent and diffusely spreading species, as *M. heterophylla*, *M. Coulteri*, *M. pulchella*, *M. integrifolia* var. *trifida*, and *M. helianthemoides* and its varieties. In *M. spinescens* and *M. robusta* the flowers are solitary and almost sessile at the ends of short lateral branches. The flowers are devoid of either bracts or bracteoles. The behavior of the pedicel in fruit provides an important diagnostic character. In the majority of the decum-

bent and diffusely spreading species, such as *M. heterophylla*, *M. pulchella*, *M. Coulteri*, *M. helianthemoides* with its varieties, and others, it is recurved in fruit, whereas in those species erect and more or less strict in habit, the pedicel is erect in fruit. An intermediate condition is found in *M. integrifolia* var. *trifida*, which is

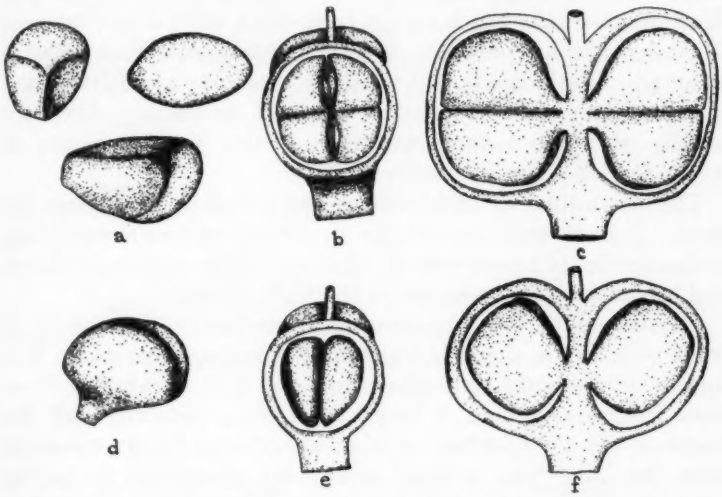

Fig. 1. Drawings showing the position and number of ovules in the two subgenera, *Eumenodora* and *Duogyne*.

a. Ovules of the subgenus *Eumenodora:* ovule seen from below on the inner angle; outer, convex surface of ovule; and inner, flat contact-surface seen from the inner angle. × 21.

b. Dorsal view of the ovary with portion of pericarp removed, showing position of ovules in *Eumenodora*. × 18.

c. Lateral view of the ovary with portion of pericarp removed, showing position of ovules in *Eumenodora*. × 21.

d. Ovule of the subgenus *Duogyne*, showing flat, inner surface. × 21.

e. Dorsal view of the ovary with portion of pericarp removed, showing position of ovules in *Duogyne*. × 18.

f. Lateral view of the ovary with portion of pericarp removed, showing position of ovules in *Duogyne*. × 21.

decumbent and diffusely spreading, but has erect pedicels in fruit. The pedicels are usually short in the early stages, but become elongated in fruit.

Calyx.—The calyx varies in length from 0.4 cm. or less, as in

M. helianthemoides var. *Engelmannii*, to nearly 2.5 cm., as in *M. longiflora*. In most of the species it is approximately equal in length to the corolla-tube, but in *M. longiflora* and *M. robusta* it is usually from one-third to one-fourth the length of the corolla-tube. Although the calyx-lobes vary in number from five to fifteen, the number is relatively constant for individual species. For example, *M. helianthemoides* has from ten to thirteen calyx-lobes, whereas *M. integrifolia* has only five or six. The calyx-lobes are variable in length, mostly linear, but in *M. robusta* they are deltoid, and in *M. africana* and *M. Coulteri* they are setaceous. They are usually entire; a notable exception occurs in *M. africana* in which the lobes are frequently cleft.

The calyx-tube is turbinate or campanulate, and generally short. It is markedly nerved, the number of nerves corresponding to the number of lobes present. The tube of the calyx is persistent and becomes slightly enlarged as the fruit matures.

Corolla.—With the exception of a few species the corolla is fairly constant in shape throughout the genus. Generally, it is subrotate or shortly infundibuliform, the tube varying in these cases from 3 to 7 mm. in length, and being generally half the length of the corolla-lobes, or in some instances barely equalling them (fig. 2d). Two or three species are exceptional in having relatively long tubes. *Menodora spinescens* var. *mohavensis* has an infundibuliform corolla-tube 10 mm. in length; *M. robusta* has an infundibuliform tube about 12 mm. long, whereas *M. longiflora* has the greatest extreme, with a hypercrateriform tube varying in length from 25 to 53 mm. (fig. 2c). In all species save one, *M. longiflora*, in which the tube is entirely glabrous, the corolla-tube is bearded within at the orifice, the slender hairs occurring mostly around the area where the filaments are inserted upon the throat.

The corolla-lobes are usually five in number, but six occasionally occur. In shape they vary from narrowly oblong to broadly obovate or ovate, as in *M. longiflora*. They are obtuse or acute, and frequently slightly or distinctly mucronate, imbricated in aestivation, and usually spreading at anthesis. They are generally glabrous, but in *M. scabra*, *M. helianthemoides*, and others they are sparsely scabrous-puberulent without.

The corolla is usually golden-yellow or white, but in some

species, as *M. heterophylla* and *M. spinescens* var. *mohavensis*, it is tinged brownish or dull purplish-red without. Engelmann noticed that the short-tubed, inodorous flowers, as those of *M. heterophylla* and *M. scabra*, are open during the day, whereas the

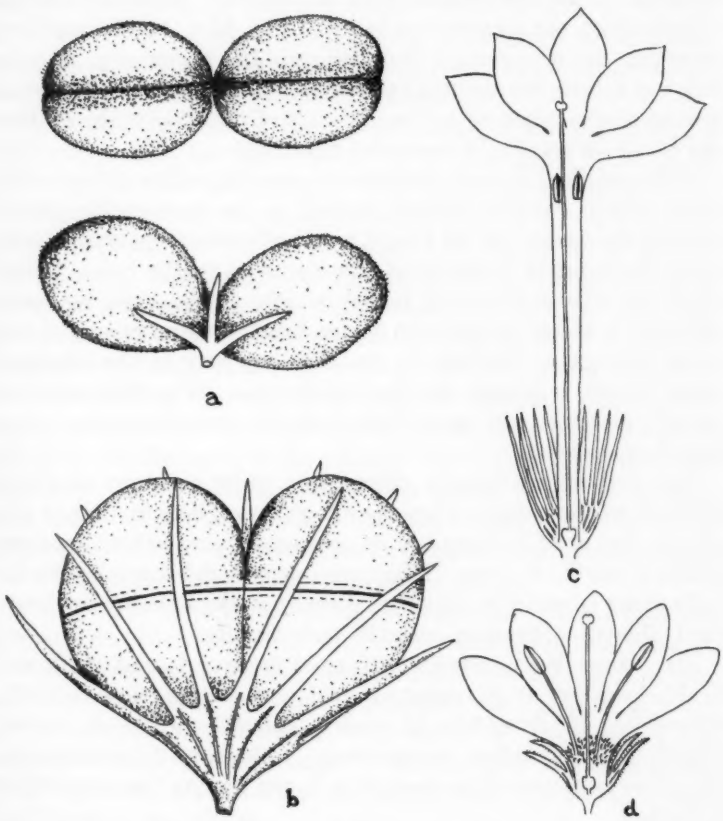

Fig. 2.

a. Fruit of the subgenus *Duogyne;* upper figure, capsule from above, showing suture along the vertical plane; lower figure, lateral surface view of capsule, showing divaricate cocci. × 3.

b. Fruit of the subgenus *Eumenodora*, lateral surface view. × 4.

c. Flower of *M. longiflora*, the corolla and calyx opened. × 1.

d. Flower of *M. Coulteri*, the corolla and calyx opened. × 1.

long-tubed, sweet-scented flowers, as of *M. longiflora*, are open at night.

Stamens.—The stamens are two in number, thus according with all other genera in the family. They are equal in length, and are inserted on the corolla-tube near the orifice. When the corolla-tube is short, the stamens are exserted (fig. 2d). In *M. longiflora*, however, the stamens are included near the orifice (fig. 2c). In this last species the anthers have such short filaments as to appear almost sessile, whereas in the majority of the species the anthers are borne on relatively elongated filaments.

Although the filaments are inserted near the orifice of the corolla, their central vascular strand, as well as the surrounding parenchymatous tissue, can be traced externally along the corolla-tube from the point of insertion of the filaments to the base. Thus, since the filaments are in reality adnate to the tube for some distance, it seems desirable in taking length-measurements of the entire stamen or filament to include that part of the staminal tissue which is adnate to the corolla-tube. The filaments are usually glabrous and erect, but those in *Menodora robusta* are densely pubescent.

The anthers are usually oblong and quite constant in shape throughout the genus. They are about 2 mm. long in most of the species, but in *M. robusta* and *M. spinescens* var. *mohavensis* they attain a length of 4 mm. They are introrse, dehiscing longitudinally along lateral slits, attached dorsally to the filament and basifixed, though appearing versatile superficially.

The connective is usually prolonged more or less at the apex. In *M. longiflora* it is triangular and very conspicuous. In *M. integrifolia*, *M. decemfida*, *M. scabra*, and *M. scoparia* it is prolonged into a rather conspicuous cylindrical protuberance. *Menodora spinescens* is an exception in not having the connective prolonged.

The pollen has been studied in all the species and varieties of *Menodora*, as well as in seventeen other genera in the family, including all the tribes and subsections in the Oleaceae, and in all instances the exine has been observed to be more or less reticulate, either regularly or irregularly (pl. 4, figs. 1–4). The pollen grain of species of *Menodora* has three germinal apertures. The size of

the grain is remarkably constant for each species, and in most species it averages from 60 to 90 μ in diameter. The smallest grains are found in *M. spinescens* (pl. 4, fig. 1), ranging from (33.75); 39.9 to 50 μ[18] in diameter, while the largest occur in *M. longiflora*, ranging in diameter from (112.55); 125 to 143.75; (162.50) μ. *Menodora robusta* (pl. 4, fig. 3) has larger reticulations than any of the other species, while *M. africana* (pl. 4, fig. 2) and *M. intricata* have the smallest type of reticulation.

The technique used in the present study of the pollen grains closely approximates that outlined by Wodehouse.[19] Herbarium material was used throughout. First the flower was boiled until sufficiently softened, after which initial process it could be preserved in 70 per cent alcohol or transferred directly to the mounting medium. When ready for mounting the specimen was transferred to a slide, where by aid of needles under the dissecting binoculars the pollen was removed from the anther. A drop of water was then added and the cover-glass was placed on the slide. A dilute solution of Amann's lactophenol mounting medium was finally placed around all sides of the cover glass and allowed to diffuse gradually towards the center.[20] By means of this stain the characters of the exine markings were brought out more clearly. The nature of the reticulation and the variation in size of the pollen grain served in part as checks or confirmatory evidence for the affinities existing between the various species.

Pistil.—The pistil in the genus *Menodora* is typically bicarpellary and accords in structure with other members of the Oleaceae. The style is simple, filiform, elongated and usually about as long as the corolla-tube. One teratological case was observed in which two free styles were found in a flower of *M. spinescens*. The stigma is usually broadly capitate and more or less emarginate. In *M. africana*, *M. spinescens*, and a few other species, it is small and more or less obtuse.

The bilocular ovary is fleshy and bilobed. The placentation is axillary. The ovules are two to four in number, collateral, and

[18] The parentheses marks indicate the extreme in size.

[19] Wodehouse, R. P. The phylogenetic value of pollen-grain characters. Ann. Bot. **42**: 896–898. 1928.

[20] Linder, D. H. An ideal mounting medium for mycologists. Science **70**: 430. 1929.

attached about half way up the placentae. The integument is very thick and fleshy and the surface becomes conspicuously reticulated as the ovule matures. The subgenera *Eumenodora* and *Duogyne* present an interesting contrast in regard to the number and arrangement of the ovules. All the species of *Eumenodora* have in each cell four ovules arranged collaterally in pairs, superimposed and horizontal in position (fig. 1 a–c). The funicles are very proximate. The ovules are compressed in two planes; because of this pressure from two sides, they are always trigonal, being flattened on the two inner faces of contact and convex on the outer third free surface. This trigonal shape persists from the development of the ovule to that of the seed. In contrast to this condition it was found that in the species belonging to the subgenus *Duogyne* there are only two ovules in each cell (fig. 1 d–f). These ovules are slightly ascending, with a dorsal raphe and a micropyle pointing below. They are likewise compressed, but because of the fact that the pressure exists in one plane only, their shape is plano-convex rather than trigonal, the inner face of contact being flattened, while the outer free surface is convex. This shape likewise persists in the contour of the mature seed.

Some confusion has arisen in the past concerning the number of ovules in each cell. One reason for this confusion is that the ovules stick together closely, and, unless a careful dissection is made, could readily be taken as two instead of four, as is the case of those species included in the subgenus *Eumenodora*. An instance of such an oversight is to be found in Bentham's original description and illustration of *Bolivaria robusta*,[21] in which the number of ovules is described as follows: "ovula in quoque loculo 2, loculum implentia . . ." Philippi[22] in 1864 described a new species, *M. linoides*, as possessing two ovules in each cell, and the description reads "loculis biovulatis," but no authentic material of this species has been examined.

Fruit.—The fruit of the genus *Menodora* at once distinguishes it from all other Oleaceous genera. It is a bilocular capsule, each loculus being referred to as a coccus. In those species belonging

[21] Bentham, G., in Hook. Lond. Jour. Bot. 5: 190. *pl. 5.* 1846.
[22] Philippi, R. A., in Linnaea 33: 174. 1864.

to the subgenus *Eumenodora* the capsule dehisces circumscissilely, namely, transversely to the vertical axis (fig. 2b). This line along which the dehiscence occurs does not become conspicuous, however, until the fruit nears maturity. At maturity each of the cocci dehisces by this horizontal suture, and the upper half becomes free. The number of mature seeds in the species in this subgenus is usually four. An exception to this may be found in *M. africana*, in which some of the seeds fail to mature. The placentae are not evident in the mature capsule of this subgenus. After fertilization the ovules greatly enlarge, extending the pericarp, and in so maturing become displaced from their original position. Thus, the mature seeds, having become displaced during development, now appear to arise from the lower inner angle at the base of each coccus. Due to the growth of the gynoecium upwards after fertilization, however, the seeds are more or less ascending rather than horizontal.

In the subgenus *Duogyne* the fruit is not a circumscissilely dehiscent capsule. In contrast, a median longitudinal suture or stricture appears in the vertical plane (fig. 2a). However, no indications of dehiscence along this suture are evident. Moreover, each valve of the capsule is two- rather than four-seeded.

In those species included in the subgenus *Eumenodora* the cocci are subglobose, smooth, glabrous, and nearly proximate (fig. 2b), whereas in the subgenus *Duogyne* the cocci are ovoid or obovoid, minutely pubescent, and conspicuously divaricate, appearing almost as separate capsules (fig. 2a).

The seeds consist of two coats, an inner, brown, smooth, subcoriaceous one, and an outer, brown, thick, spongy, variously reticulated one. Some species, as *M. heterophylla*, *M. longiflora*, *M. scoparia*, and others, have a coarse, deep-grooved reticulation, whereas others, such as *M. scabra* and *M. spinescens*, possess a very minute reticulation which appears almost smooth to the naked eye. In some species the reticulation is quite regular, in others exceedingly irregular.

In those species comprising the subgenus *Eumenodora* the seeds are, as in the case of the ovules, trigonal. In the subgenus *Duogyne*, on the other hand, the seeds are plano-convex, as were the ovules.

Embryo.—The embryo in all cases is straight, large, and completely fills the seed. The cotyledons are flat, the radicle is inferior, and endosperm is completely lacking.

GEOGRAPHICAL DISTRIBUTION

The genus *Menodora* presents a very interesting problem in plant distribution. Of the seventeen species and thirteen varieties recognized in this paper, nine species and eleven varieties occur in North America, six species and one variety in South America, and two species and one variety are found in Africa,

Fig. 3. Map showing general distribution of *Menodora*.

Map reproduced by permission of American Map Co.

one of the species, *M. heterophylla*, being found in North America and having its variety in Africa. There are, accordingly, three distinct areas of distribution: (1) southwestern United States and Mexico, (2) central and southern South America, and (3) South Africa. Despite this extensive tricontinental distribution, it will

be noted that the genus inhabits a definite belt ranging between the extremes of 18° to 45° North and South latitudes (fig. 3). Furthermore, in those three areas of distribution a similar set of environmental conditions exists—similar rainfall and temperature extremes as well as topographic conditions. It may be generally stated that the genus *Menodora* is limited to arid or semi-arid rocky plateaus or stony slopes in mountainous regions. It should be stated that the deserts and semi-deserts of the southwestern United States, the arid Mexican, southern and central Bolivian, the central and eastern Argentine plateaus, the arid central Chilean region, the South African Karroo tableland, and the region north of it, are all topographically and environmentally similar, and all have a similar characteristic xerophytic type of vegetation.[23] The various modes of external morphological response of species of *Menodora* to these xerophytic conditions are extremely interesting. The leaves have become variously reduced, subcoriaceous with incurved margins, and the stomata occur below the surface plane of the epidermis; in *M. robusta* the tips of the branches have become conical, producing a spiny appearance, the leaves on the main branches are greatly reduced, and most of the chlorophyll production has been taken over by the stout, fleshy, green stems. True spines may develop in *M. spinescens* and its variety *mohavensis*.

The restricted range of most of the species is another interesting phase in the matter of the present geographical distribution of the genus. In respect to the number of forms, the genus is best represented in Mexico, where four species and seven varieties are endemic, in addition to four other species and varieties extending into Mexico from the United States (fig. 4). The greatest number of individuals, however, has been collected in the southwestern United States, particularly in New Mexico, Arizona, and Texas. Many of the species and varieties on the Mexican plateau have very circumscribed areas of distribution (fig. 4). For example, *M. helianthemoides* is known only from the state of Puebla; *M. helianthemoides* var. *parviflora* from the states of Puebla and Hidalgo; *M. helianthemoides* var. *humilis* from San Luis Potosi;

[23] Schimper, A. F. W., transl. by R. W. Fischer. Plant geography, pp. 604–649. Oxford, 1903.

Fig. 4. Map of the geographical distribution of *Menodora* in western United States and Mexico.

M. helianthemoides.
M. helianthemoides var. *humilis.*
M. helianthemoides var. *magniflora.*
M. helianthemoides var. *Engelmannii.*
M. helianthemoides var. *parviflora.*
M. Coulteri.
M. Coulteri var. *minima.*
M. mexicana.
M. heterophylla.
M. scabra.
M. scabra var. *laevis.*
M. scabra var. *ramosissima.*
M. scabra var. *longituba.*
M. decemfida var. *longifolia.*
M. longiflora.
M. scoparia.
M. intricata.
M. intricata var. *Purpusii.*
M. spinescens.
M. spinescens var. *mohavensis.*

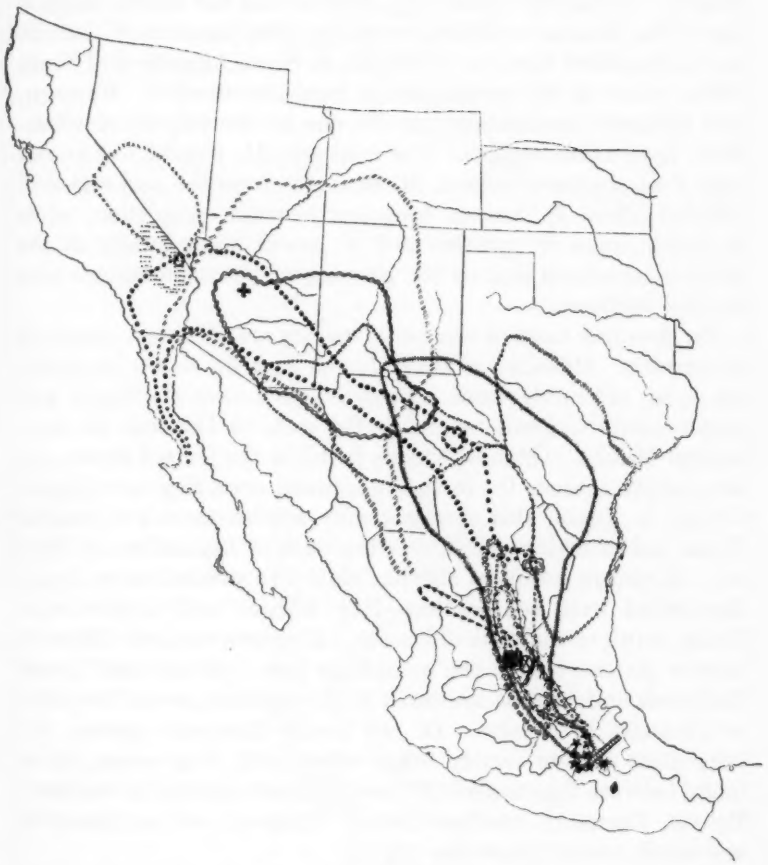

Fig. 4.

M. intricata from Minas de San Rafael in the west-central portion of the state of San Luis Potosi, while *M. intricata* var. *Purpusii* has been found only in the mountains near Tehuacan in southern Puebla. *Menodora Coulteri* var. *minima* has the widest range of any of the Mexican endemics, extending from the state of Coahuila to south-central Mexico. Likewise, in South America and South Africa most of the species are of local distribution. However, this apparent localization may be due to the paucity of collections from these regions. For instance, *M. pulchella* is known only from southern Bolivia, *M. decemfida* from the arid region of Central Chile, *M. robusta* from southeastern Argentina, while in South Africa *M. africana* and *M. juncea* occur locally on the Karroo tablelands and on the plateaus of the mountainous area to the northeast.

On the other hand, a number of species are of more widespread occurrence. *Menodora scabra* of North America covers the greatest area, extending from southern and Lower California and south-central Colorado south to the state of Durango in west-central Mexico. Of those species found in the United States, *M. heterophylla* extends the farthest eastward, occurring near Corpus Christi in Texas; this species covers southwestern and central Texas and extends southward to the state of Tamaulipas in Mexico. *Menodora longiflora* also has quite an extended range, being distributed from southeastern New Mexico and southwestern Texas, south to the state of Puebla. *Menodora scoparia* follows a narrow plateau belt in the mountains from southern and Lower California and Arizona southeast to the southern part of the state of Coahuila in Mexico. Of the South American species, *M. integrifolia* and its variety *trifida* cover fairly large areas, being found between the parallels 20° and 35° South latitude in southern Bolivia, Paraguay, southern Brazil, Uruguay, and northeastern and north central Argentina (fig. 5).

The genus *Menodora* at the present time occupies three remote areas of distribution, but in all probability had a more continuous geographical range at least before the end of the Cretaceous period. The most logical source of evidence explaining this present interrupted distribution lies in the postulation of a land-bridge once connecting South America and Africa, which geologists have

Fig. 5. Map of the geographical distribution of *Menodora* in South America.

C *M. pulchella.*
∝ *M. integrifolia.*
β *M. integrifolia* var. *trifida.*
= *M. Hassleriana.*
⋈ *M. pinnatisecta.*
S *M. decemfida.*
ℏ *M. robusta.*

named Gondwana. It is thought that at one time there existed but one continent; there is evidence, both paleontological and paleontoclimatical, that at the beginning of the Paleozoic era such was the case. This hypothesis is based on the relatively recent development of the large oceans, and upon the world-wide past distribution of various plants and animals.[24] More particularly the postulation of a land connection between South America and Africa has been set forth to explain the past and present distribution of flora and fauna. In connection with this there are numerous bits of evidence that lend support to the idea of the previous existence of Gondwana. The first relates mainly to widespread deposits of the Gangamopteris flora of Permian age. "This flora occurs throughout the southern hemisphere, and paleobotanists hold that it could have been so widely distributed only across a continuous land. . . Without this continent, on the other hand, paleontologists cannot explain the known distribution of Permian land life, and further, its presence is equally necessary for the interpretation of the peculiar distribution of marine fauna beginning certainly with the Devonian and ending in the Jurassic."[25] Another piece of evidence pointing to the previous existence of a land connection between South America and Africa is the zone known as the "Mid-Atlantic Swell." Daly says: "The zone where the New and Old Worlds were torn apart is plausibly regarded as the so-called Mid-Atlantic Swell, which is a long and broad 'ridge' on the ocean's floor; its height averages about one mile, or sixteen hundred meters. . . The ridge or swell is in the middle of the Atlantic basin, about half-way between Brazil and Africa. . . The Ascension Island and other volcanoes on the swell have erupted fragments of typical continental rocks to the surface. The swell may, therefore, conceivably represent a long strip of the original continent, a strip left behind when that continent was torn into fragments, which slid away, respectively, to westward and to eastward. Other masses, like the rugged pile of the Azores, may also represent sunken pieces of the original continent."[26] Additional evidence that such a

[24] Daly, R. A. Our mobile earth. pp. 311–315. 1926.

[25] Schuchert, C. C. Text-book of geology. Part II, pp. 432–433. *fig. 145.* ed. 2. 1924.

[26] Daly, R. A. *loc. cit.* pp. 279–280. 1926.

continent may have existed is to be found in the striking correspondence between the geology of South Africa and that of Argentina. Daly says in reference to this: "A dozen peculiar features of the one region are repeated in the other. . . . In both of these mutually distant lands, thick deposits were made by glaciers, away back in the Paleozoic era, many tens of millions of years before the familiar last Glacial period began in North America. These ancient glacial deposits of the southern hemisphere have been hardened into tough rock."[27] Thus, various bits of evidence lend support to the hypothesis of this lost continent.

The postulation of this land-bridge may explain the range of the genus in three continents, and especially in South America and South Africa. This hypothetical lost continent might also account for the presence of *M. heterophylla* in North America and its variety in South Africa. However, according to geological records, this hypothetical land connection between South America and Africa was obliterated by upper Cretaceous time.[28] Consequently it would seem that the genus *Menodora*, in order to have attained this widespread distribution, and particularly in having a species and a closely related variety at present occurring on two distant continents, must necessarily have been in existence at least before the end of the Cretaceous period. Such a situation would seem highly probable, especially since, according to paleontological records, angiosperms had attained a world-wide distribution by the earlier half of the Cretaceous.[29] This would presuppose the supposition that they were existing in the Jurassic or even in the Triassic period. Although there are no known Cretaceous records of fossil Oleaceae that are worthy of credence, Berry[30] points out that "It is obvious from the early Eocene occurrence of leaves of *Fraxinus* associated with characteristic fruits, that the family must have been evolved before the close of the Upper Cretaceous but none of the genera have any well-marked or abundant known representation until Tertiary times."

[27] *loc. cit.* pp. 285–286.

[28] Schuchert, C. C. Text-book of geology. Part II, pp. 510, 547–548, 610, ed. 2. 1924.

[29] *loc. cit.* pp. 550–561.

[30] Berry, E. W., in Am. Phil. Soc. Proc. 53: 243. 1914.

No species of the genus *Menodora* have been found so far in the fossil state. This may be accounted for by the fact that the plants grow in arid regions, especially on high plateaus; they apparently come and go without being preserved, because such conditions seem to be unfavorable for preservation.

From the evidence just presented, it seems not unlikely that the genus *Menodora* was at one time, probably not later than the end of the Cretaceous period, distributed at least from South America to Africa, this range being made possible by the existence of the hypothetical land-bridge, Gondwana. The existence of this lost continent might explain the present distribution of *M. heterophylla* in North America and its variety in South Africa, as well as the extended distribution over the three continents in which the genus is now found.

A somewhat parallel example of similar discontinuous distribution is cited by Hill[21] in his discussion of the genus *Vernonia*.

SYSTEMATIC POSITION

The genus *Menodora* belongs to the tribe Jasmineae of the Oleaceae. A similarity in floral structure exists between the genera *Menodora*, *Jasminum*, and *Nyctanthes*, as shown by the variable number of calyx- and corolla-lobes, the imbricated aestivation, the prolonged corolla-tube, and the short, included anthers. A further evidence of this affinity is to be seen in the large reticulations on the exine of the pollen-grain. The species of *Menodora* best illustrating these relationships are *M. longiflora* and *M. robusta*.

PHYLOGENY

There are two chief lines of development manifest in the genus *Menodora*, which are emphasized by the subgeneric categories, namely, *Eumenodora* and *Duogyne*. The characteristics of the first are (1) the four-ovulate cells of the ovary with trigonal-shaped ovules, (2) the circumscissile dehiscent nature of the fruit, (3) the proximate subglobose cocci, and (4) the unarmed habit. In contrast to these characters the distinctive features of the second are (1) the biovulate cells of the ovary with plano-convex

[21] Hill, A. W. Proc. Internat. Cong. Pl. Sciences, Ithaca, **2**: 1480–1481, 1486. 1929.

ovules, (2) the seemingly indehiscent, non-circumscissile capsule, each coccus marked with a vertical suture, (3) the divaricate, almost separate, ovoid or obovoid cocci, and (4) the spinose habit.

The fact that the subgenus *Duogyne* has a reduction to two ovules in each cell of the ovary, has a very specialized habit, and has a very limited range in distribution over a relatively recent area geologically, namely, the Mohave Desert and the adjacent region, would indicate that it is the younger of the two subgenera. It should be considered as a subgenus which has been derived through reduction from the older and more widespread *Eumenodora* (fig. 6).

This instance seems to be one, at least, which well illustrates the Age-and-Area hypothesis.[32] The subgenus *Eumenodora* may be interpreted as relatively older than the subgenus *Duogyne*. The former has a much more widespread distribution and a larger number of species and varieties than the latter, being represented in three continents. This situation would suggest that it has had a longer period of evolution than the subgenus *Duogyne*. Further evidence in support of the antiquity of the former subgenus lies in the fact that one of the species belonging to this group, *M. heterophylla*, occurs with its variety in two widely separated continents, namely, North America and Africa. Since this distribution may be explained by the supposition of the existence of a land-bridge forming a ready means of dispersal for species between the continents, it may be supposed that *M. heterophylla* extended from North America to South Africa over the postulated lost continent, Gondwana, before the end of the Cretaceous. If this were true, and there is geological and paleontological evidence for supposing that such may have been the case, then the implication would be that the subgenus *Eumenodora* had been evolved before the obliteration of Gondwana. On the other hand, there is no evidence of glaciation for that portion of Nevada and California in which the single species, *M. spinescens*, and its variety, comprising the subgenus *Duogyne*, occur to indicate that they are relic forms, and, in addition, the region now occupied by this subgenus is a relatively recent one, which facts would lead one to suppose that its present distribution correlated with its repre-

[32] Willis, J. C. Age and area. Cambridge, 1922.

sentation in only one species and variety is a result of its relatively more recent evolution. Finally, the subgenus *Duogyne* shows a reduction from four to two in the number of ovules and seeds in each cell, and this fact, together with those already discussed, would seem to indicate that it is a relatively recent group, having been derived from *Eumenodora*.

Within the subgenus *Eumenodora* certain tendencies are shown. On the one hand, there are those species with pedicels erect in fruit and, on the other, those with the pedicels recurved (fig. 6). Usually, the former species are of erect habit with strict stems, whereas the latter are of more or less decumbent growth with the stems diffuse and spreading. An intermediate condition exists, as would be expected, in which the plants are decumbent with diffuse spreading stems, but have erect pedicels in fruit. An example is *M. integrifolia* var. *trifida*. It would seem that those species with the pedicels recurved in fruit were the more recently evolved, since they manifest a reduced type of inflorescence, the flowers appearing to be solitary, but actually being arranged in a remotely flowered dichasial cyme. They may be considered as having had their inflorescence derived from a well-defined type of dichasial cyme, such as is found in many of those species of the genus, as *M. scabra*, *M. longiflora*, and others.

The recurved-pedicel type is thought to have come from an ancestor, whose condition resembled *M. integrifolia* var. *trifida*, which is an intermediate phase and which in turn may have been derived from a condition similar to that now occurring in *M. integrifolia* (fig. 6). *Menodora helianthemoides* and *M. Coulteri* represent entire-leaved phases of development in the recurved-pedicel group, whereas *M. heterophylla*, *M. pulchella*, and *M. africana* comprise examples of various off-shoots from a pinnatifid-leaved stock.

There occurs, moreover, within the group of erect-pedicel types a series of derivative forms which tend towards successive reduction of foliar organs. A type, such as occurs in *M. scabra*, in which all the leaves are foliose, may be considered as the ancestral form. Variations within this species tend towards a series of branching forms in which the upper leaves become smaller. This branching becomes further manifest in *M. decemfida* and its variety *longifolia;*

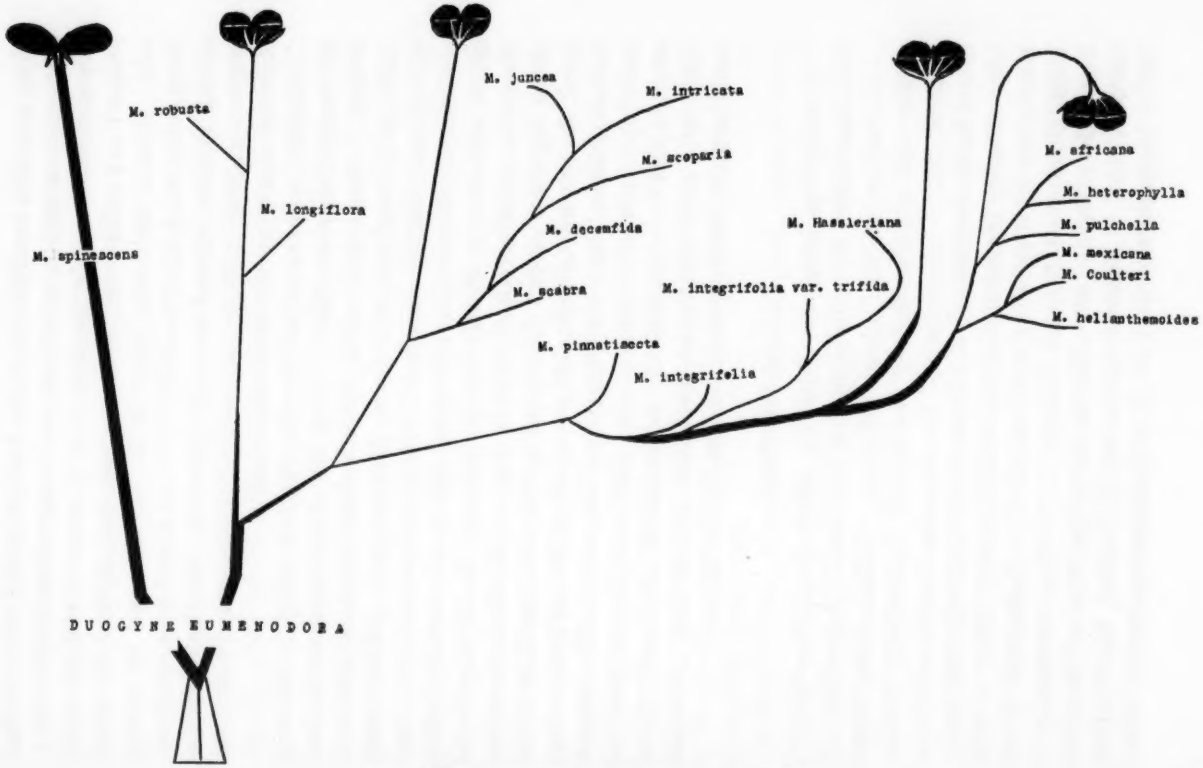

Fig. 6. Phylogenetic chart of the genus *Menodora*.

along with this condition the leaves become farther removed from each other on the elongated internodes, and become rudimentary. It would seem possible, therefore, that *M. scoparia* with the leaves reduced to a rudimentary state has been derived from *M. decemfida*. Further reduction exists in *M. intricata* and its variety *Purpusii* in which all of the leaves have lost their foliose condition, having become reduced to mere rudiments. Finally, reduction becomes extreme in *M. juncea*, in which the leaves are practically obsolete, appearing only as minute scales.

Another tendency within the erect-pedicel group is shown in the corolla characters (fig. 6). One line of development has been towards a long-tubed corolla, with included anthers, such as is found in *M. longiflora*, *M. robusta*, *M. spinescens*, and its variety *mohavensis*. On the other hand, remaining species in the erect-pedicel group have evolved along the line of short-tubed corollas, either subrotate or shortly infundibuliform. In all these forms the orifice of the corolla is pilose within, and the stamens are exserted beyond the tube. The fact that the same condition occurs in all the species belonging to the nodding-pedicel group would indicate that one has been derived from the other; in this instance, probably the nodding-pedicel type has been derived from the erect-pedicel type, because the former shows a reduced inflorescence, and a probably more specialized pedicel that may easily have been derived from the kind found in the latter.

ABBREVIATIONS

In citing specimens the following abbreviations for herbaria have been used: A = Herbarium of the Arnold Arboretum; AL = Herbarium of the Albany Museum, Grahamstown, South Africa; AR = Herbarium of the Desert Laboratory, Tucson, Arizona; BER = Herbarium of the Botanical Garden and Museum of Berlin-Dahlem; C = University of California Herbarium; DS = Dudley Herbarium of Stanford University; DUR = Natal Herbarium at Durban, South Africa; F = Herbarium of the Field Museum of Natural History; G = Gray Herbarium of Harvard University; M = Herbarium of the Missouri Botanical Garden; NAT = National Herbarium at Pretoria, South Africa; NY = Herbarium of the New York Botanical Garden; P = Her-

barium of the Philadelphia Academy of Natural Sciences; POM = Herbarium of Pomona College; St. B. = Herbarium of the Santa Barbara Museum; US = Herbarium of the United States National Museum.

Taxonomy

Menodora Humb. & Bonpl. Pl. Aequin. **2**: 98. *pl. 110.* 1809; Linn. Sp. Pl. [Roem. & Schult.] ed. nov. **1**: 53. 1817; Linn. Syst. Veg. [Spreng.] ed. 16. **1**: 70. 1825; HBK. Nov. Gen. et Sp. Pl. **7**: 199. 1825; D. Don in Edinb. New Phil. Jour. **6**: 48. 1828–29; G. Don, Gen. Hist. Dichl. Pl. **4**: 58. 1838; Griseb. Gen. et Sp. Gentian. 20. 1839; Endl. Gen. Pl. 571. 1841; A. DC. in DC. Prodr. **8**: 316. 1844; A. Gray in Am. Jour. Sci. II. **14**: 43. 1852; Walp. Ann. Bot. **5**: 487. 1858; Harvey, Gen. So. Afr. Pl. ed. 2. 220. 1868; Eichler in Mart. Fl. Bras. **6**: 318. 1868; Benth. & Hook. Gen. Pl. **2**: 674. 1876; A. Gray, Syn. Fl. N. Am. 2^1: 78. 1878; Coulter in Contr. U. S. Nat. Herb. **2**: 261. 1892; Knoblauch in Engler & Prantl, Nat. Pflanzenf. 4^2: 13. 1895; Small, Fl. S. E. U. S. ed. 1. 916. 1903, and ed. 2. 917. 1913; Macloskie in Rept. Princeton Univ. Exp. to Patagonia (Bot.). 8^2: 65. 1905; Harvey in Fl. Cap. **4**: 484. 1909; Arechavelata in Anal. Mus. Nac. Montevideo **7**: 54. 1909; Reiche, Fl. Chile **5**: 103. 1910; Wooton & Standley in Contr. U. S. Nat. Herb. **19**: 497. 1915; Rydberg, Fl. Rocky Mts. 656. 1917, and ed. 2. 656. 1922; Jepson, Man. Fl. Pl. Cal. 760. 1925.

Bolivaria Cham. & Schlecht. in Linnaea **1**: 207. 1826; G. Don, Gen. Hist. Dichl. Pl. **4**: 58. 1838; Griseb. Gen. et Sp. Gentian. 20. 1839; A. DC. in DC. Prodr. **8**: 315. 1844; Schlecht. in Linnaea **26**: 473. 1853.

Calyptrospermum A. Dietrich in Linn. Sp. Pl. [A. Dietrich] ed. 6. **1**: 226. 1831.

Low decumbent, or erect, nearly herbaceous to shrubby and suffruticose, glabrous or pubescent, spinose or unarmed perennials. Leaves alternate or opposite, sessile or petioled, decurrent on the stem, exstipulate, membranaceous, fleshy or subcoriaceous, linear, elliptic-oblong to suborbicular, simple, entire or pinnately bi- to multi-lobed or cleft. Inflorescence centrifugal, in one- to many-flowered corymbose, paniculate, or di- to tri-chasial cymes (when

one-flowered, terminal or axillary in the upper axils). Pedicels recurved or erect in fruit. Calyx gamosepalous, persistent; tube short, turbinate or campanulate, 5–15-parted; lobes setaceous, linear-subulate to cuneate, simple or cleft, glabrous or pubescent, acuminate to obtuse. Corolla gamopetalous, subrotate, campanulate, infundibuliform, or salverform, pilose or glabrous within the throat, the 5–6 lobes imbricate, broadly obovate to narrowly elliptic-oblong, acuminate to obtuse. Stamens 2, inserted near the base or above the middle of the throat of the corolla, included or exserted; filaments long or short, glabrous or pubescent at the base; anthers bilocular, oblong or elliptic-oblong, dorsally attached, basifixed, the cells dehiscing laterally, connective sometimes mucronate at the apex. Ovary superior, obcordate-emarginate, glabrous, inserted on a short gynophore, bilocular. Style filiform, erect, glabrous, about equalling the length of the corolla, longer than the anthers, exserted. Stigma depressed-capitate, slightly obtuse or emarginate. Ovules 4, rarely 2, in each cell, paired, collateral, attached laterally near the middle of the placentae, ascending, descending, or horizontal, anatropous. Capsule didymous, bilocular, membranaceous, glabrous or pubescent, each cell subglobose, ovoid or obovoid, dehiscing circumscissilely, or indehiscent. Seeds usually 4, sometimes 2, in each cell, paired, trigonal or plano-convex, with two coats, the outer spongy with an irregular network, the inner coriaceous, more or less smooth. Endosperm absent. Embryo large, cotyledons flat or plano-convex, radicle short, inferior.

Type species: *Menodora helianthemoides* Humb. & Bonpl. Pl. Aequin. **2**: 98. *pl. 110.* 1809.

KEY TO THE SUBGENERA

A. Plants unarmed (appearing spinescent in *M. robusta*); ovules 4 in each cell; capsule dehiscing circumscissilely, the cocci proximate, more or less globose; seeds trigonal, 4 in each cell. . . *Subgenus Eumenodora* spp. 1–16

AA. Plants spinose; ovules 2 in each cell; capsule not circumscissile, seemingly indehiscent, each coccus marked with a vertical suture or stricture; cocci very divaricate (almost separate), ovoid or obovoid; seeds plano-convex, 2 in each cell. . . . . *Subgenus Duogyne* sp. 17

KEY TO THE SPECIES AND VARIETIES OF MENODORA

A. Plants diffuse or decumbent; flowers solitary, terminal or axillary, the pedicels recurved in fruit.

a. Leaves entire throughout.
b. Plants always more or less pubescent.
c. Leaves mostly ovate to elliptic-oblong.
d. Stems densely hirsute-pilose, with conspicuous, spreading hairs.
e. Plants 1.2–2.5 dm. high; corolla 12–14 mm. long.....
.....*1. M. helianthemoides*
ee. Plants 0.3–0.8 dm. high; corolla 9–12 mm. long.....
.....*1a. M. helianthemoides* var. *humilis*
dd. Stems hirtellous-scabrous or scabrous-puberulent, with inconspicuous, short or closely appressed hairs.
e. Corolla 14–17 mm. long....*1b. M. helianthemoides* var. *magniflora*
ee. Corolla 9–12 mm. long.
f. Stems densely scabrous-puberulent, appearing grayish-white; calyx 3–4 mm. long; mature fruit 5–6 mm. broad.
.....*1c. M. helianthemoides* var. *Engelmannii*
ff. Stems sparsely hirtellous-scabrous, with inconspicuous hairs; calyx 5–8 mm. long; mature fruit about 10 mm. broad.....*1d. M. helianthemoides* var. *parviflora*
cc. Leaves mostly linear to oblong-lanceolate.
d. Calyx 5–11 mm. long; corolla 13–17 mm. long.....*2. M. Coulteri*
dd. Calyx 3–7 mm. long; corolla 7–8.5 mm. long.....
.....*2a. M. Coulteri* var. *minima*
bb. Plants entirely glabrous.....*3. M. mexicana*
aa. Some or all of the leaves cleft.
b. Leaf-segments narrowly linear, less than 1 mm. broad; calyx-lobes frequently cleft.....*4. M. africana*
bb. Leaf-segments lanceolate to obovate, 1–4 mm. broad; calyx-lobes always entire.
c. Calyx-lobes 10–14; leaf-segments lanceolate to oblanceolate, acute; upper leaves frequently entire.
d. Plants mostly diffusely spreading; stems glabrous to slightly scabrous; corolla-lobes slightly or not at all mucronate; upper leaves frequently larger than the lower; leaf below the node subtending the pedicel, equalling or surpassing the calyx; species of North America.....*5. M. heterophylla*
dd. Plants more or less strict; stems densely scabrous; corolla-lobes mostly conspicuously mucronate; upper leaves smaller and more reduced than the lower; leaf below the node subtending the pedicel not approximating the calyx; species of South Africa.....*5a. M. heterophylla* var. *australis*
cc. Calyx-lobes 6–7; leaf-segments oblong to obovate, obtuse; upper leaves never entire.....*6. M. pulchella*
AA. Plants mostly erect; flowers in few- to many-flowered cymes (rarely appearing solitary), the pedicels erect in fruit.
a. Plants unarmed (appearing spinescent in *M. robusta*); ovules 4 in each cell; capsule dehiscing circumscissilely; the cocci proximate, more or less globose; seeds 4 in each coccus.
b. All leaves foliose, the leaf blades well developed.
c. Corolla-tube short, 2.5–7 mm. long, subrotate to shortly infundibuliform, pilose at the orifice.

d. Calyx-lobes 5–6 (rarely 7).
e. Leaves acute.
f. Plants erect; flowers in few to many-flowered cymes.....
.....*7. M. integrifolia*
ff. Plants decumbent or diffusely spreading; flowers appearing solitary or in remote dichasial cymes.....
.....*7a. M. integrifolia* var. *trifida*
ee. Leaves obtuse.....*8. M. Hassleriana*
dd. Calyx-lobes usually 8–12 (rarely 7).
e. Leaves mostly pinnatisect.....*9. M. pinnatisecta*
ee. Leaves entire.
f. Plants relatively low, subcaespitose, flax-like; stems mostly simple and subherbaceous.
g. Leaves mostly linear or linear-lanceolate; corolla-lobes oblong to narrowly obovate, obtuse, slightly mucronate.....*10. M. scabra*
gg. Leaves mostly ovate, oblong-elliptic, or oblong-lanceolate; corolla-lobes broadly ovate to subovate, acute, distinctly mucronate.....*10a. M. scabra* var. *laevis*
ff. Plants relatively tall; stems very much branched.
g. Leaves mostly elliptic-oblong or oblong-lanceolate.
h. Corolla-tube short, 4.5–5 mm. long.....
.....*10b. M. scabra* var. *ramosissima*
hh. Corolla-tube relatively long, 6–7 mm. long.....
.....*10c. M. scabra* var. *longituba*
gg. Leaves mostly linear or linear-lanceolate.
h. Corolla-lobes oblong-lanceolate, 3–4 mm. broad; corolla-tube about 6 mm. long; species of South America.....*11. M. decemfida*
hh. Corolla-lobes oblong to obovate, 5–8 mm. broad; corolla-tube 4–5 mm. long; species of Mexico and Texas.....*11a. M. decemfida* var. *longifolia*
cc. Corolla-tube elongated, 25–53 mm. long, salverform, entirely glabrous within.....*12. M. longiflora*
bb. Leaves, at least the upper ones, bracteate, becoming rudimentary.
c. Upper leaves bracteate, becoming rudimentary, lower leaves foliose.....*13. M. scoparia*
cc. All of the leaves bract-like, the leaf blades much reduced.
d. Corolla-tube short, 4–5 mm. long.
e. Stems very much ribbed and intricate; calyx-lobes 7–11; species of North America.
f. Plants mostly glabrous, 2.5–4 dm. high; corolla 10–12 mm. long.....*14. M. intricata*
ff. Plants scabrous, 0.6–1.2 dm. high; corolla 8–10 mm. long.
.....*14a. M. intricata* var. *Purpusii*
ee. Stems not conspicuously ribbed and intricate; calyx-lobes 5; species of Africa.....*15. M. juncea*
dd. Corolla-tube elongated, about 12 mm. long.....*16. M. robusta*

aa. Plants spinose; ovules 2 in each cell; capsule not circumscissile, seemingly indehiscent, each coccus marked with a vertical suture or stricture; cocci strongly divaricate (almost separate), ovoid or obovoid; seeds 2 in each coccus.

b. Corolla-tube 4–6 mm. long, narrowly infundibuliform, more or less abruptly expanded at the orifice.....*17. M. spinescens*

bb. Corolla-tube 10–12 mm. long, broadly infundibuliform, gradually ampliated at the orifice.....*17a. M. spinescens* var. *mohavensis*

1. M. helianthemoides Humb. & Bonpl. Pl. Aequin. **2**: 98. *pl. 110.* 1809; Planches de Bot. **4**: *pl. 103.* 1823; Kunth in HBK. Nov. Gen. et Sp. Pl. **7**: 199. 1825; G. Don, Gen. Hist. Dichl. Pl. **4**: 58. 1838; Steud. Nom. Bot. ed. 2. **2**: 124. 1841; A. DC. in DC. Prodr. **8**: 316. 1844; A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Walp. Ann. Bot. **5**: 487. 1858; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881, and **4**: 67. 1886; S. Watson in Proc. Am. Acad. **18**: 112. 1883; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Standl. in Contr. U. S. Nat. Herb. **23**: 1138. 1924.

A branching, decumbent, suffruticose perennial, 1.2–2.5 dm. high; stems numerous, slender, slightly angled, divergently and diffusely spreading, opposite, and conspicuously and densely hirsute-pilose; leaves opposite, numerous, crowded, slightly petiolate, oblong-elliptic to suborbiculate, including the petiole, 5–22 mm. long, 3–10 mm. broad, obtuse, mucronate, entire, densely hirsute-pilose, submembranaceous; flowers large, relatively few, solitary, terminal, in remotely flowered dichasial cymes; pedicels slender, 5–10 mm. long, densely hirsute-pilose, recurved in fruit; calyx campanulate, 8–14 mm. long, hirsute-pilose; calyx-tube 1.5–2 mm. long, in anthesis 1.5–2 mm. broad, in fruit about 3 mm. broad; lobes 10–13, equal or unequal, setaceous, linear-lanceolate to linear-spatulate, acute to acuminate, entire, 7–10 mm. long, 0.25–1.3 mm. broad; corolla shortly infundibuliform or subrotate, 12–14 mm. long, golden yellow; corolla-tube short, 3–4 mm. long, about 4 mm. broad at the orifice, densely pilose within; lobes 5, elliptic-oblong, obtuse or slightly acutish, 10–12 mm. long, about 4 mm. broad, irregularly hirsute-pilose without; stamens exserted, 7–10 mm. long; filaments glabrous, slightly mucronate at the apex; pollen grain finely reticulated, (72.5); 75–93.75; (100.0) μ in diameter; pistil about 10 mm. long; ovules 4 in each cell; stigma broadly capitate; capsule 7–8 mm. long, about 10–12

mm. broad; seeds 4 in each cell, finely and irregularly reticulate, about 5 mm. long, 3 mm. broad.

Distribution: southeastern Mexico.

Specimens examined:

MEXICO:

PUEBLA: in vicinity of San Luis Tultitlanapa, near Oaxaca, June, 1908, *Purpus 3392* (C, F, G, M, NY, US); El Riego, June, 1905, *Purpus 1319* (C, F, G, M, NY); near Tehuacan, Aug. 1 and 2, 1901, *Rose & Hay 5931* (US).

1a. Var. **humilis** Steyermark, n. var.[33]

A dwarf suffruticose perennial, 0.3–0.8 dm. high; leaves, including the petiole, 2–11 mm. long, 1–5 mm. broad, acute; calyx 4–7 mm. long, lobes 2–6 mm. long; corolla 9–12 mm. long, with the lobes 8–10 mm. long; capsule 5–6 mm. long, 9–10 mm. broad.

In other respects similar to the species.

Distribution: San Luis Potosi, Mexico.

Specimens examined:

MEXICO:

SAN LUIS POTOSI: region of San Luis Potosi, 22° N. Lat., alt. 1829–2439 m., 1878, *Parry & Palmer 571*, in part (F, G, M, TYPE) and *570*, in part (F).

1b. Var. **magniflora** Steyermark, n. var.[34]

Stems moderately scabrous; leaves 5–16 mm. long, 1.5–6 mm. broad, scaberulent; calyx moderately scabrous; corolla 14–17 mm. long, lobes broadly ovate, 13–14 mm. long, 7–9 mm. broad; capsule 8–9 mm. long, about 15 mm. broad.

In other respects similar to the species.

Distribution: San Luis Potosi, Mexico.

[33] Var. **humilis** Steyermark, var. nov., humilis, suffruticosa, perennis, 0.3–0.8 dm. alta; foliis, petiolis includentibus, 2–11 mm. longis, 1–5 mm. latis, calyce 4–7 mm. longo, lobis 2–6 mm. longis; corolla 9–12 mm. longa, lobis 8–10 mm. longis; capsula 5–6 mm. longa, 9–10 mm. lata.—TYPE collected in region of San Luis Potosi, state of San Luis Potosi, Mexico, alt. 1829–2439 m., 1878, *Parry & Palmer 571*, in part (M).

[34] Var. **magniflora** Steyermark, var. nov., caulibus moderate scabrosis; foliis 5–16 mm. longis, 1.5–6 mm. latis, scaberulentis; calyce moderate scabroso; corolla 14–17 mm. longa, lobis late obovatis, 13–14 mm. longis, 7–9 mm. latis; capsula 8–9 mm. longa, circiter 15 mm. lata.—TYPE collected in region of San Luis Potosi, state of San Luis Potosi, Mexico, alt. 1829–2439 m., 1878, *Parry & Palmer 570*, in part (M).

Specimens examined:

MEXICO:

SAN LUIS POTOSI: in region of San Luis Potosi, 22° N. Lat., alt. 1829–2439 m., 1878, *Parry & Palmer 570*, in part (F, G, M TYPE, P, US); San Luis Potosi, 1877, *Schaffner 503* (NY); in montibus, Morules, San Luis Potosi, Sept., 1876, *Schaffner* (NY); San Luis Potosi, 1878, *Schaffner 68* (NY); 1879, *Schaffner 503* (US); in montibus prope Morules, ex convalli San Luis Potosi, October, 1876, *Schaffner 68* (G).

WITHOUT LOCALITY: *Coulter 937* (G); des collines de la Presa, 1902, *Dugès 18* (G).

1c. Var. **Engelmannii** Steyermark, n. var.[35] Pl. 5, fig. 1

A dwarf suffruticose perennial, 0.4–0.6 dm. high; stems densely scaberulent, appearing grayish-white; leaves ovate to linear-lanceolate, including the petiole, 2.5–8 mm. long, 1–3 mm. broad, acute; pedicels scaberulent; calyx 3–4 mm. long, slightly scabrous, lobes 2.5–3 mm. long; corolla 10–11 mm. long, lobes 6–7 mm. long; capsule about 4 mm. long, about 5–6 mm. broad.

In other respects similar to the species.

The type of this variety, a plant collected by Gregg in Saltillo, Mexico, in 1848, was designated and described in manuscript as a new species by Dr. George Engelmann.

Distribution: southern Coahuila to Hidalgo, Mexico.

Specimens examined:

MEXICO:

COAHUILA: valley near Saltillo, May 7, 1848, *Gregg 44* (G, M TYPE); Saltillo, 1898, *Ed. Palmer 164* (C, F, M, NY, US).

SAN LUIS POTOSI: region of San Luis Potosi, 22° N. Lat., alt. 1829–2439 m., 1878, *Parry & Palmer 571*, in part (F, G, M).

HIDALGO: Ixmiquilpan, *Rose, Painter & Rose 9007* (NY).

ZACATECAS: arroyos in hills, Cedros, July, 1908, *Lloyd 140* (US).

[35] Var. **Engelmannii** Steyermark, var. nov., humilis, suffruticosa perennis, 0.4–0.6 dm. alta; caulibus scaberulentissimis, cinereo-albidis; foliis ovatis vel lineari-lanceolatis, petiolis includentibus, 2.5–8 mm. longis, 1–3 mm. latis, acutis; pedicellis scaberulentis; calyce 3–4 mm. longo, subscabroso, lobis 2.5–3 mm. longis; corolla 10–11 mm. longa, lobis 6–7 mm. longis; capsula 4 mm. longa, 5–6 mm. lata.—TYPE collected in valley, near Saltillo, state of Coahuila, Mexico, May 7, 1848, *Gregg 44* (M).

1d. Var. **parviflora** Greenman in Proc. Am. Acad. **34**: 569. 1899.

A decumbent suffruticose perennial, 0.4–2 dm. high, more or less hirtellous-scabrous throughout, with inconspicuous hairs; leaves slightly fleshy, including the petiole, 5–19 mm. long, 1.5–6 mm. broad, acute; calyx 5–8 mm. long, lobes 3–6 mm. long, 0.3–1 mm. broad; corolla 9–12 mm. long, with 5 narrowly oblong, acutish lobes 7–8 mm. long, 3–4 mm. broad; corolla-tube 4–5 mm. long, about 2–3 mm. broad at the orifice; stamens 7–8 mm. long; anthers conspicuously mucronate at the apex; pistil about 8 mm. long; capsule about 6 mm. long, about 10 mm. broad.

Distribution: Hidalgo and Puebla, Mexico.

Specimens examined:

MEXICO:

HIDALGO: bare hills above Pachuca, alt. 2591 m., July 30, 1896, *Pringle 6918* (C, F, G TYPE, M, NY, P, Pom, US); Pachuca, alt. 2134–2439 m., July, 1903, *Purpus 437* (M, C, Pom, US), and *434*, in part (C); between Pachuca and Real del Monte, July 19, 1905, *Rose, Painter & Rose 8712* (US).

PUEBLA: Moria, 1800 m., June, 1909, *Arsène* (F).

2. M. Coulteri A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Walp. Ann. Bot. **5**: 487. 1858; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881; S. Watson in Proc. Am. Acad. **18**: 112. 1883; Standl. in Contr. U. S. Nat. Herb. **23**: 1138. 1924.

A branching, decumbent or somewhat erect, suffruticose perennial, 1.5–2 dm. high; stems opposite, numerous, slender, more or less terete, divergently and diffusely spreading to erect, usually scaberulent; leaves opposite, numerous, rather crowded, subcoriaceous, narrowed at the base into a short petiole, linear to oblanceolate, including the petiole, 2–18 mm. long, 1–3 mm. broad, acute to acuminate, entire, glabrous or sparsely scaberulent; flowers large, relatively few, solitary, terminal; pedicels slender, 3–10 mm. long, glabrous or slightly roughened, recurved in fruit; calyx campanulate, 5–11 mm. long, glabrous or sparsely scaberulent; calyx-tube 1.3–2 mm. long, in anthesis 1.1–2 mm. broad, in fruit 2–3 mm. broad, mostly glabrous, sometimes sparsely scaberulent; lobes 10–15, linear, entire, setiform, acuminate, 4–10

mm. long, 0.2–0.5 mm. broad, sparsely hirtellous on the margins; corolla subrotate, 13–17 mm. long; corolla-tube short, 3–5 mm. long, 3–4 mm. broad at the orifice, densely pilose within; lobes 5–6, oblong or elliptic, obtuse, 10–13 mm. long, 4–6 mm. broad; stamens exserted, 7–9 mm. long; filaments glabrous, anthers slightly mucronate at the apex, the connective prolonged into a short, cylindrical protuberance; pollen grain finely and regularly reticulated, (75); 93.75–106.25; (112.5) μ in diameter; pistil about 10–14 mm. long; ovules 4 in each cell; stigma broadly capitate; capsule 5–6 mm. long, about 10 mm. broad; seeds 4 in each cell, rather finely and irregularly reticulated, about 4 mm. long, 1.5–2 mm. broad.

Distribution: Coahuila and Nuevo Leon to Hidalgo, Mexico.

Specimens examined:

MEXICO:

NUEVO LEON: Jasmincillo del Monte, 15 mi. w. of Icamole, Feb. 3, 1907, *Safford 1263* (US).

SAN LUIS POTOSI: in region of San Luis Potosi, 22° N. Lat., alt. 1829–2439 m., 1878, *Parry & Palmer 571*, in part (US).

HIDALGO: Zimapan, *Coulter 938* (G TYPE); rocky slopes, Ixmiquilpan, Aug. 1905, *Purpus 1447* (C, F, G, M, NY, Pom); near Ixmiquilpan, 1905, *Rose, Painter & Rose 8311* (US).

COAHUILA: Saltillo, April 15–30, 1898, *Ed. Palmer 34* (C, F, G, M, NY, US).

2a. Var. **minima** Steyermark, n. var.[36]

Leaves lanceolate to ovate-lanceolate, including the petiole, 2–6 mm. long, 1–2 mm. broad; flowers small; calyx 3–7 mm. long, lobes 2–6 mm. long; corolla 7–8.5 mm. long, lobes about 5 mm. long, 2.5–3 mm. broad, mucronate; stamens about 6 mm. long; pistil about 7 mm. long.

In other respects similar to the species.

Distribution: Coahuila and Nuevo Leon south to south-central Mexico.

[36] Var. **minima** Steyermark, var. nov., foliis lanceolatis vel ovato-lanceolatis, petiolis includentibus, 2–6 mm. longis, 1–2 mm. latis; floribus minimis; calyce 3–7 mm. longo, lobis 2–6 mm. longis; corolla 7–8.5 mm. longa, lobis circiter 5 mm. longis, 2.5–3 mm. latis, mucronatis; staminibus circiter 6 mm. longis; pistillo circiter 7 mm. longo.—TYPE collected near Arroyos, Cedros, state of Zacatecas, June, 1908, *Kirkwood 20* (M).

Specimens examined:

MEXICO:

COAHUILA AND NUEVO LEON: Feb.–Oct., 1880, *Ed. Palmer* (G, P).

SAN LUIS POTOSI: in region of San Luis Potosi, 22° N. Lat., alt. 1829–2439 m., 1878, *Parry & Palmer 571*, in part (M) and *300½* (G).

ZACATECAS: near arroyos, Cedros, June, 1908, *Kirkwood 20* (F, M TYPE).

HIDALGO: rocky slopes, Ixmiquilpan, Aug. 1905, *Purpus 1447* (G, POM); Pachuca, alt. 2134–2439 m., 1903, *Purpus 434*, in part (C).

WITHOUT LOCALITY: Sierra de la Paila, Oct., 1910, *Purpus 5020* (C).

3. M. mexicana (A. DC.) A. Gray in Am. Jour. Sci. II. **14**: 45. 1852; Walp. Ann. Bot. **5**: 488. 1858; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881; Standl. in Contr. U. S. Nat. Herb. **23**: 1138. 1924.

Bolivaria Mexicana A. DC. in DC. Prodr. **8**: 315. 1844.

A nearly herbaceous, erect perennial, about 1.5 dm. high; stems numerous, slender, strict, angled, glabrous; leaves not crowded, opposite, slightly petiolate, linear to oblong-lanceolate, including the petiole, 6–17 mm. long, 1–5 mm. broad, entire, acute, glabrous, subcoriaceous; flowers few, solitary, terminal; pedicels slender, 6–17 mm. long, glabrous, recurved in fruit; calyx campanulate, 10–12 mm. long, glabrous; calyx-tube about 3 mm. long, in anthesis about 2 mm. broad, in fruit about 4 mm. broad, glabrous; lobes 10–12, linear, setiform, acuminate, 5–10 mm. long, 0.2–0.5 mm. broad, glabrous; corolla subrotate, 13–15 mm. long; corolla-tube short, about 3 mm. long, about 4 mm. broad at the orifice, pilose within; lobes 5, elliptic-oblong, obtuse, mucronate, 10–12 mm. long, 5–6 mm. broad; stamens exserted, about 10 mm. long; pistil about 12 mm. long; stigma capitate; capsule about 6 mm. long, 10–12 mm. broad.

Distribution: Oaxaca, Mexico.

No specimens seen. Description compiled.

MEXICO: near Oaxaca, July, *Andrieux 228* (Herb. DC. TYPE, M photograph of type).

4. **M. africana** Hooker in Hook. Ic. Pl. *pl. 586.* 1842; A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Walp. Ann. Bot. **5**: 487. 1858; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Wood, Natal Pl. 3^2: 17. *pl. 240.* 1902; Harvey in Fl. Cap. **4**: 484. 1907. Pl. 4, fig. 2; pl. 5, fig. 2.

An erect or slightly decumbent, nearly herbaceous perennial, 0.6–2.5 dm. high; stems numerous, diffuse, freely branched, mostly terete, sparingly to densely scabrous; leaves opposite or alternate, numerous, fleshy, subsessile to distinctly petiolate, including the petiole, 3–10 mm. long, about 4–6 mm. broad, multifid, heather-like, the segments narrowly linear, 1–5 mm. long, about 0.3 mm. broad, acute, glabrous or slightly scabrous on the margins; flowers relatively numerous, pedicels solitary, terminal, slender, 5–10 mm. long, scabrous, recurved in fruit; calyx campanulate, 5–11 mm. long, glabrous to densely scabrous; calyx-tube about 1–3 mm. long, about 2 mm. broad, becoming 4 mm. broad in fruit; lobes 10–14, narrowly linear, acute, entire or cleft, 4–7 mm. long, 0.3 mm. broad; corolla subrotate, 11–17 mm. long, yellow, corolla-tube short, 2–3.5 mm. long, pilose at the orifice within; lobes 5, obovate, obtuse, slightly to conspicuously mucronate, 8–12 mm. long, 4–7 mm. broad; stamens exserted, 8–10 mm. long; filaments glabrous, connective not prolonged at the apex; pollen grain small, very finely and regularly reticulated, 48.75–56.25; (63.75) μ in diameter; pistil 9–14 mm. long; ovules 4 in each cell; stigma small, capitate; capsule 7–8 mm. long, 12–15 mm. broad; seeds usually 2 or 3 in each cell, one or more failing to develop, about 8 mm. long, about 4.5 mm. broad.

Distribution: South Africa, from the Kalahari Desert region east to Transvaal and Natal and south to the Cape Province.

Specimens examined:

AFRICA:

UNION OF SOUTH AFRICA:

CAPE PROVINCE: Tÿger Kop, Hay district, Feb. 1927, *Wilman* (AL).

NATAL: near Dundee, alt. 1220–1525 m., Nov. 1896, *Pegler* (NAT); Leeuwport, Oct. 1918, *Rogers 22393* (DUR); in graminosis near Colenso, alt. 1500 m., Sept. 27, 1893, *Schlechter 3369* (AL, BER); ½ mile from Syndicate Farm, Dundee, Indumeni Mt.,

alt. 1311.5 m., March 10, 1926, *Truscott 157* (NAT); bank of Tugela, Weenen Co., alt. 1220 m., Jan. 2, 1886, *Wood 3550* (DUR); bank of Tugela near Colenso, alt. 915 m., Oct. 23, 1888, *Wood 758*, and alt. 1220 m., *Wood 758* (BER); ad ripas fluminis, Tugela River, near Colenso, alt. 915 m., Oct. 1888, *Wood* (AL); Wagon Hill, near Ladysmith, alt. 915–1220 m., Nov. 27, 1900, *Wood 7948* (F, P); near Ladysmith, alt. 1006.5 m., Feb. 14, 1895, *Wood 5506* (M).

ORANGE FREE STATE: Kimberly, July, 1912, *Moran 86* (AL); Kroonstad, Oct. 1929, *Port 228* (NAT).

TRANSVAAL: Town Commonage, Christiana, District Bloemhof, Feb. 14, 1912, *Burtt-Davy 12480* (NAT); Vaal River, near Hebron, alt. 1159 m., 1892, *Flanagan 1472* (NAT); slopes between Kaap and Crocodile Rivers, alt. 610 m., Sept. 28, 1890, *Galpin 1071* (AL); grassy plains, Queen's River, Barberton, alt. 610 m., Nov. 15, 1890, *Galpin 1071* (NAT); plains near Crocodile Poort, alt. 610 m., Sept. 28, 1890, *Galpin 1071* (US); Vereeniging, alt. 1448.75 m., Nov.–Dec., 1898, *Gilfillan 148* (NAT); Modderfontein, Dec., 1904, *Haagner* (AL); Bloemhof, Nov. 1916, *Miss Lloyd* (AL); Arcadia, Pretoria, Nov. 29, 1915, *Murray* (NAT); Hatherly, March 20, 1905, *Rogers 109* (AL); Arcadia, Pretoria, Nov. 11, 1913, *Stent 9563* (NAT); on flats near Barberton, alt. 762.5 m., Oct. 1906, *Thorncroft 646* (DUR); Onderstepoort, Pretoria, *Veterinary Research Laboratory 25* (NAT); near Lydenburg, Oct. 1887, *Wilms* (BER).

KALAHARI REGION: Derde Poort, Oct. 18, 1904, *Leendertz 369* (AL).

BRITISH BECHUANALAND: Armoed's Vlakte, Vryburg, alt. 1207.8 m., Oct. 7, 1920, *Mogg 8024* (NAT).

GRIQUALAND WEST: in arenosis, Barkly-west, alt. 1200 m., Feb. 1886, *Marloth 258* (BER).

WITHOUT STATE: *Burchell 2478, 2960* (G); March, 1920, *Elliott* (NAT); *Government Herbarium, Department of Agriculture 14389* (NAT); February, 1920, *Moran* (NAT).

5. M. heterophylla Moric. ex A. DC. in DC. Prodr. **8**: 316. 1844; A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Walp. Ann. Bot. **5**: 487. 1858; A. Gray, Syn. Fl. N. Am. **2**[1]: 78. 1878;

Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881; Oliver in Hook. Ic. Pl. III. **5**: 47. *pl. 1459*. 1884; Coulter in Contr. U. S. Nat. Herb. **1**: 43. 1890, and **2**: 261. 1892; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Harvey in Fl. Cap. **4**: 484. 1907; Small, Fl. S. E. U. S. ed. 1. 916. 1903, and ed. 2. 917. 1913; Standl. in Contr. U. S. Nat. Herb. **23**: 1137. 1924.

Pl. 4, figs. 11–12; pl. 6, fig. 1.

M. pinnatifida Mart. in Ann. Sci. Nat. Bot. III. **19**: 365. 1853.

Bolivaria Grisebachii Scheele in Linnaea **25**: 254. 1852.

B. pinnatifida Schlecht. in Linnaea **26**: 474. 1853.

A diffuse, decumbent, subherbaceous perennial, 0.4–2.5 dm. high; stems numerous, slender, slightly angled, sparsely hispidulous; leaves opposite, slightly petiolate, numerous, crowded, submembranaceous, linear to oblong-lanceolate, acute, entire or pinnately 3–7-cleft or -lobed, including the petiole, 5–40 mm. long, 2–30 mm. broad, the segments linear-lanceolate to obovate, 3–25 mm. long, glabrous except for the slightly hirtellous margins; flowers relatively few, pedicels solitary, terminal, slender, 5–8 mm. long, scaberulent, recurved in fruit; calyx campanulate, 6–11 mm. long; calyx-tube 1–3 mm. long, in anthesis about 1.5–2 mm. broad, in fruit 4–5 mm. broad, scaberulent; lobes 10–14, linear, acute, entire, 5–10 mm. long, 0.5–1 mm. broad, hirtellous on the margins; corolla shortly infundibuliform, 8–17 mm. long, light yellow to reddish-purple; corolla-tube short, 2–5 mm. long, about 5 mm. broad at the orifice, sparsely pilose near the base of the throat within; lobes 5–6, obovate, 6–12 mm. long, 3.5–6 mm. broad, obtuse, slightly mucronate; stamens exserted, about 8–10 mm. long; filaments glabrous, connective not conspicuously prolonged at the apex; pollen grain moderately and regularly reticulated (67.25); 75–83.75; (90.0) μ in diameter; pistil about 10 mm. long; ovules 4 in each cell; stigma capitate; capsule 6–10 mm. long, 10–18 mm. broad; seeds 4 in each cell, 5–7 mm. long, about 4 mm. broad, coarsely and rather irregularly reticulated.

Distribution: central Texas south to Nuevo Leon and Tamaulipas, Mexico.

Specimens examined:

UNITED STATES:

TEXAS: in field, San Antonio, Aug. 23, 1906, *Ball 955* (US);

between Laredo and Bejar, 1828, *Berlandier 1461* (M); Arica, Nov. 1828, *Berlandier 516* (G); *Bigelow 79* (F); sandy soil, Austin, Feb. 1890, *Bodin* (M); Llano, May 12–15, 1899, *Bray 319* (US); common in barrens, San Antonio, March 24, 1902, *Bush 1181* (G, M, US); Spofford Junction, March 21, 1900, *Canby 162½* (G, P, US); tropical life zone, Bexar Co., April 17, 1911, *Clemens & Clemens 488* (C, M, POM); tropical life zone, San Antonio, Bexar Co., April 19, 1911, *Clemens & Clemens 490* (M, POM); tropical life zone, San Antonio, Bexar Co., June 20, 1911, *Clemens & Clemens 489* (POM); San Diego, 1884, *Croft 13* (NY); Painted Cave, Rio Grande River, March 12, 1893, *Davy 41* (C); Spofford Junction, March 12, 1893, *Davy 30* (C); along railroad, Victoria, Victoria Co., April 7, 1900, *Eggert* (G, M); hills, Austin, May 17, 1872, *Hall 293* (F, M, NY, POM, US); Corpus Christi, Nueces Co., alt. 0–12.2 m., March 5–12, 1894, *Heller 1390* (C, G, M, NY, P, US); 1894, *Heller* (US); Calallen, March 26, 1920, *High 80* (M); Bexar Co., 1903, *Jermy 55* (M, NY, US); Bexar Co., 1904, *Jermy 35* (NY); San Antonio, *Jermy 164* (G); San Antonio, *Jermy 262* (G); Threadgill Valley, Gillespie Co., *Jermy 447* (US); San Antonio, *Jermy* (NY, US); Del Rio, April 20, 1930, *M. E. Jones 26718* (M); Lampasas, Oct. 29, 18—, *Joor* (M); San Antonio to Laredo, March 26, 1885, *Kiddes* (G, US); Reynoldsville, Cameron Co., April 13, 1905, *Lewton 176* (US); April, 1828, *Lindheimer* (M); 1849–51, *Lindheimer* (POM); New Braunfels, 1846, *Lindheimer 454* (C, F, G, M, P, US); arid soil on the Cibolo, July, 1847, *Lindheimer 454* (M), *421* (G); on clayey soil, Agua Dulce, Matagorda, Feb. 1845, *Lindheimer 383a* (G); Guadeloupe, Victoria, Feb. 1845, *Lindheimer 383c* (M); 15 mi. w. of New Braunfels, Oct. 1846, *Lindheimer 218* (G); 1846, *Lindheimer 455* (C, G, P); Ballinger, 1889, *Nealley 378a* (US); Roma, 1889, *Nealley 262* (US); Corpus Christi, May, 1913, *Orcutt 5858* (M); Laredo, Feb.–March, 1913, *Orcutt 5594* (M); southwest Texas, Sept. 1879–Oct. 1880, *Ed. Palmer 791* (US); southwest Texas, Sept. 1879–Oct. 1880, *Ed. Palmer 790* (US); San Antonio, Sept. 1879, *Ed. Palmer 790* (G, P); Laredo, Rio Grande River, 180 miles from San Antonio, Aug. 1–20, 1879, *Ed. Palmer 791* (M); Sutherland Springs, Wilson Co., Aug. 1879, *Ed. Palmer 791* (G); dry open ground, Corpus Christi, Nueces Co., March 8, 1917, *E. J. Palmer 11214* (M); dry

open ground, calcareous soil, Sweetwater, Nolan Co., May 27, 1918, *E. J. Palmer 13726* (M); dry calcareous soil, Sabinal, Uvalde Co., June 8, 1916, *E. J. Palmer 10118* (M); dry calcareous soil, San Antonio, March 16, 1916, *E. J. Palmer 9178* (M); dry rocky ground, near Uvalde, Uvalde Co., April 28, 1928, *E. J. Palmer 33608* (M); Mexican Boundary Survey, *Parry, Bigelow, Wright & Schott 1101* (NY); Marble Falls, Aug. 10, 1892, *Plank* (NY); Del Rio, Dec. 7, 1891, *Plank* (NY); sandy prairies, Brown Co., April, 1882, *Reverchon 1328* (US); sandy soils, Brown to Tom Green Co., up to Callahan, April, 1882, *Reverchon 1328* (F, M); dry soils, Kimble Co., May, 1885, *Reverchon 1328* (C, F, G, M, NY, US); Tamarcensis, *Riddell* (NY); sandy soil, Loma Alta, alt. 9.15 m., June 1, 1923, *Runyon 548* (US); western Texas, *Schott* (F); *Schott 3344* (F); San Marcos and vicinity, spring of 1897, *Stanfield* (NY); chaparral, 5 mi. w. of Del Rio, Valverde Co., June 9, 1931, *Moore & Steyermark 3006* (M); Colorado, May 16, 1908, *Tracy 8087* (F, G, NY, US); Spofford, April 7, 1900, *Trelease 26* (M); vicinity of San Antonio, April, 1919, *von Schrenk 1* (M); San Antonio, 1900, *Wilkinson 7* (M); San Antonio, 1897, *Wilkinson 7* (M); Reynoldsville, April 15, 1905, *Williamson 176* (P); *Wright* (NY); May–Oct. 1849, *Wright 562* (F, G, US); near Austin, Oct. 12, 1913, *Young* (M); abundant in dry open ground, university campus, Austin, March 22, 1918, *Young* (G).

MEXICO:

TAMAULIPAS: dry valley, east of Camargo, June 1, 1847, *Gregg 883* (G, M, NY); San Fernando to Jimenez, Feb. 26–27, 1902, *Nelson 6602* (G, US); vicinity of Victoria, alt. 320 m., Feb. 1–April 9, 1907, *Ed. Palmer 85* (C, F, M, US); 25 miles south of Matamoros, June 29, 1919, *Wooton* (US).

NUEVO LEON: valley, Monterey, July 29, 1889, *Pringle 2408* (C, F, M, NY, P, US); El Carriro, near Monterey, Sept. 4, 1904, *Pringle 13456* (US).

5a. Var. australis Steyermark, n. var.[37] Pl. 6, fig. 2.

A relatively strict perennial, 0.7–1.3 dm. high; stems harshly

[37] Var. **australis** Steyermark, var. nov., relative stricta perennis, 0.7–1.3 dm. alta; caulibus aspere scabris; foliis minoribus et reductioribus, 3–16 mm. longis, 1–7 mm. latis, scabrioribus; pedicellis dense scabris; calycis lobis 2–8 mm. longis, scabris; corollae lobis plerumque manifeste mucronatis.—TYPE collected on grassy turf, near Rustenburg, alt. 1220 m., Aug., 1903, *Pegler 950* (BER).

scabrous; leaves smaller and more reduced, 3–16 mm. long, 1–7 mm. broad, the segments 2–7 mm. long, more scabrous; pedicels densely scabrous; calyx-lobes 2–8 mm. long, scabrous; corolla-lobes mostly conspicuously mucronate.

Distribution: Transvaal and Kalahari region, South Africa.

The opinion has been generally held in the past that this South African plant was conspecific with the North American *M. heterophylla*. Oliver,[38] describing and illustrating the South African plant for the first time from material collected in the Transvaal, Matebe Valley, by Dr. Holub, considered it as conspecific with the plant from the New World, stating, "although we have no fruiting specimens from South Africa, yet there seems no ground to doubt the identity of this Transvaal plant . . . with North American specimens of which we have an ample series," and "now the interest of the case is heightened by Dr. Holub's discovery of a second South African species actually conspecific with a North American one."

Although the Old and the New World plants, in general, show striking similarity, yet careful examination reveals several points of difference. The American plant is, on the average, taller, more diffusely spreading than the dwarfed, stricter African specimen. The leaves of the former are generally larger and more scabrous than those of the latter. The upper leaves of the American plant are frequently much larger than those lower on the cauline axis, whereas in the African plant the upper leaves are usually smaller and more reduced, but never larger, than those lower on the stem. Further, the stems and pedicels of the African plant are decidedly more densely scabrous with larger excrescences than those of the American specimen. Also, the corolla-lobes of the latter are, at the most, only slightly mucronate, whereas those of the African plant are generally conspicuously mucronate. Finally, it is to be noted that in the American plant the leaf immediately below the node subtending the pedicel of the flower constantly equals or surpasses the calyx, whereas in the African plant the leaf in the same position never approximates the calyx.

This is a very striking instance, seemingly, of parallel development, and, although there are morphological differences existing

[38] Oliver in Hook. Icon. III. 5: 47. *pl. 1459.* 1884.

between these plants, they do not seem to the writer of distinct or sufficiently large import to warrant specific differentiation.

Specimens examined:

SOUTH AFRICA:

TRANSVAAL: Klerksdorp, Cape Province, Nov., *Convent Sisters 28* (AL); grassy plains near race course, Rustenburg, June 11, 1928, *Galpin 9668* (NAT); on the border between Marico and Rustenburg district, near Wonderfontein, Oct. 25, 1907, *Gray 4131* (NAT); Klerksdorp, Cape Province, Jan. 1913, *Lucy 11* (AL); turf, from Pretoria to Woodstock, Rustenburg, alt. 1220 m., Sept. 17, 1903, *Pegler 950* (AL, NAT); grassy turf, near Rustenburg, alt. 1220 m., Aug. 1903, *Pegler 950* (BER TYPE); grassy turf, near Rustenburg, alt. 1220 m., Sept., 1903, *Pegler 950* (AL); Zeerust, alt. 1220 m., Dec. 1927, *Thode* (DUR).

BECHUANALAND PROTECTORATE: Lobatsi, alt. 1189.5 m., Oct. 1913, *Rogers 6225* (AL, NAT); Mochudi, April, 1914, *Rogers 6900* (DUR).

6. M. pulchella Markgraf in Notizbl. **8**: 219. 1922.

A dwarf, decumbent, suffruticose perennial, 0.4–0.8 dm. high; stems numerous, slender, angled, reddish-tinged, sparsely scaberulent on the margins of the decurrent petioles; leaves opposite, numerous, crowded, shortly petiolate, including the petiole, 6–9 mm. long, 3–6 mm. broad, minutely hirtellous on the margins, subcoriaceous, bi–tri-lobed, lobes oblong to obovate, 1.5–3 mm. long, 1–2.5 mm. broad, obtuse; flowers relatively few; pedicels solitary, terminal, 2–4 mm. long, glabrous, recurved in fruit; calyx campanulate, 5–6 mm. long; calyx-tube 2–3 mm. long, in anthesis 2 mm. broad, in fruit 3–4 mm. broad, glabrous; lobes 6–7, linear, 3–4 mm. long, 0.3–0.7 mm. broad, entire, acutish, sparsely ciliate on the margins; corolla subrotate to shortly infundibuliform, about 14 mm. long, golden-yellow to reddish, corolla-tube about 6 mm. long, 3 mm. broad at the orifice, sparsely pilose near the base of the throat within; lobes 5, broadly oblong, obtuse, about 8–10 mm. long, 4–5 mm. broad; stamens slightly exserted, about 7 mm. long; filaments glabrous, pollen regularly reticulate, 62.5–70.0 (75.0) μ in diameter; pistil 7–10 mm. long; ovules 4 in each cell; stigma small; capsule 3–4 mm. long, 5–6 mm. broad; seeds 4 in each cell (mature seeds not seen).

Distribution: southern Bolivia.

Specimens examined:

South America:

Bolivia: Condorhuassu bei Tarija, 3200 m., Feb. 6, 1904, *Fiebrig 2984* (F cotype).

7. M. integrifolia (Cham. & Schlecht.) Steud. Nom. Bot. ed. 2, **2**: 124. 1841; A. Gray in Am. Jour. Sci. II. **14**: 43. 1852; Walp. Ann. Bot. **5**: 487. 1858; Eichler in Mart. Fl. Bras. 6^1: 318. *pl. 85. fig. 1.* 1868; Griseb. Symb. 224. 1879; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Arechavaleta in Anal. Mus. Nac. Montevideo **7**: 61. 1909; Hicken, Chlor. Plat. Argent. 183. 1910.

Bolivaria integrifolia Cham. & Schlecht. in Linnaea **1**: 268. *pl. 4. fig. 1.* 1826; Hook. & Arn. in Hooker's Jour. Bot. **1**: 284. 1834; G. Don, Gen. Hist. Dichl. Pl. **4**: 58. 1838; Griseb. Gen. et Sp. Gentian. 20. 1839; A. DC. in DC. Prodr. **8**: 315. 1844.

Calyptrospermum integrifolium A. Dietr. in Linnaeus, Sp. Pl. [A. Dietrich] ed. 6. **1**: 227. 1831.

An erect, mostly unbranched, nearly herbaceous perennial, 2.7–4 dm. high; stems relatively few, simple, elongated, slender, angled, subherbaceous above, slightly branched and opposite at the base, glabrous; leaves opposite, rather numerous, linear, slightly petiolate, linear to linear-lanceolate, including the petiole, 10–32 mm. long, 1–3 mm. broad, submembranaceous, acute, mucronate, glabrous, mostly entire or bi–tri-fid; flowers usually numerous, in paniculate dichasial cymes; pedicels slender, 3–12 mm. long, glabrous, erect in fruit; calyx narrowly campanulate, 4–8 mm. long, glabrous or nearly so; calyx-tube 2–3 mm. long, in anthesis 1.5–2 mm. broad, in fruit about 3 mm. broad; lobes usually 5–6(–7), linear to linear-lanceolate, acute to acuminate, entire, rather bifid at the apex, 2.5–6 mm. long, 0.3–0.8 mm. broad, mostly glabrous; corolla shortly infundibuliform, 10–12 mm. long, corolla-tube about 4 mm. long, 2.5–3 mm. broad at the orifice, sparsely pilose at the base of the filaments within; lobes 5, narrowly elliptic-oblong, obtuse, 6–7 mm. long, 2.5–3 mm. broad; stamens slightly exserted, about 8 mm. long; filaments glabrous, connective prolonged at the apex into a short, cylindrical, blunt,

knob-like protuberance; pollen grain finely and regularly reticulate, (58.75); 75–87.5; (93.75) μ in diameter; pistil about 9 mm. long; ovules 4 in each cell; stigma capitate; capsule about 5 mm. long, twice as broad; seeds 4 in each cell, coarsely and regularly reticulate, 4–5 mm. long, 3 mm. broad.

Distribution: southern Bolivia to Paraguay, and south to Uruguay.

Specimens examined:

SOUTH AMERICA:

BOLIVIA: Sierra de La Cruz, alt. 2000 m., 1892, *Kuntze* (F, NY).

PARAGUAY: in the Camp Bord. de v. Rias, Dec. 4, 1928, *Jörgensen 4045* (M).

URUGUAY [Brasilio meridionalis]: *Sellow* (C COTYPE).

7a. Var. **trifida** (Cham. & Schlecht.) Steyermark, n. comb. Pl. 7, fig. 1.

Menodora trifida (Cham. & Schlecht.) Steud. Nom. Bot. ed. 2. **2**: 124. 1841; A. Gray in Am. Jour. Sci. II. **14**: 43. 1852; Walp. Ann. Bot. **5**: 487. 1858; Eichler in Mart. Fl. Bras. 6^1: 318. *pl. 35. fig. 2.* 1868; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Chodat in Bull. Herb. Boiss. II. **3**: 915. 1903; Macloskie in Rept. Princeton Univ. Exp. to Patagonia (Bot.) 8^2: 658. 1905; Hicken, Chlor. Plat. Argent. 183. 1910.

Bolivaria trifida Cham. & Schlecht. in Linnaea **1**: 209. 1826; Graham in Edinb. New Phil. Jour. **10**: 167. 1830–31; G. Don, Gen. Hist. Dichl. Pl. **4**: 58. 1838; Griseb. Gen. et Sp. Gentian. 20. 1839; A. DC. in DC. Prodr. **8**: 315. 1844.

Calyptrospermum trifidum (Cham. & Schlecht.) A. Dietr. in Linn. Sp. Pl. [A. Dietr.] ed. 6. **1**: 226. 1831.

A diffusely spreading or decumbent, branching, subherbaceous perennial, 0.6–2.5 dm. high; stems glabrous to sparsely puberulent; leaves linear to oblanceolate, including the petiole, 3–22 mm. long, 0.5–11 mm. broad, mostly glabrous, entire to bi- to multi-lobed or cleft, lobes linear to oblong-lanceolate, 1.5–10 mm. long, 0.3–3 mm. broad, acute, mucronate; flowers solitary, terminal, in remotely flowered dichasial cymes; pedicels glabrous to sparsely puberulent; corolla 8–13 mm. long; corolla-tube 4–5 mm. long, 3.5–4 mm. broad at the orifice; pollen grain (62.50); 66.25–75.0; (81.25) μ in diameter.

In other respects similar to the species.

Distribution: central Bolivia and northern Paraguay south to Central Argentina.

Specimens examined:

SOUTH AMERICA:

BOLIVIA: Bolivian plateau, 1891, *Bang 942* (F, G, M, NY, P, US); Padcaya, alt. 2000–2100 m., Dec. 12, 1903, *Fiebrig 2530* (F, M), and *2531* (M); Cerrito, Ciudad Cochabamba, alt. 2600 m., Dec. 13, 1928, *Steinbach 8761* (M).

PARAGUAY: between Rio Apa and Rio Aquidaban, Dec. 3, 1908, *Fiebrig 4368* (G); Paraguay, Feb. 20–25, 1903, *Fiebrig 908* (F, G, US); in regione collium, Cerros de Paraguay, Dec. 1900, *Hassler 6475* (G); in Campa Tacuaral, Oct. 1885–95, *Hassler 1281* (NY).

ARGENTINA: Cordoba, Dec., 1891, *Kuntze* (F, NY); Sierra de San Luis, Jan. 19–Feb. 19, 1895, *Kurtz 8456* (NY); Cordoba, Jan. 25, *Lossen 305* (G).

URUGUAY: Tacuarembo, March, 1913, *Osten 6625b* (G).

8. **M. Hassleriana** Chodat in Bull. Herb. Boiss. II. 3: 915. 1903.

A diffuse and decumbent to erect, subherbaceous perennial, 0.9–2 dm. high; stems numerous, slender, slightly angled, sparsely puberulent; leaves opposite to alternate, slightly petiolate, numerous, crowded, submembranaceous, elliptic-oblong to spatulate, obtuse, slightly mucronate, entire or 3–7-cleft or lobed, including the petiole, 5–20 mm. long, 2–12 mm. broad, the segments linear-lanceolate to spatulate, 3–8 mm. long, 1–3 mm. broad, glabrous; flowers relatively few; pedicels solitary, terminal, slender, 3–8 mm. long, scaberulent, erect in fruit; calyx campanulate, 5–8 mm. long; calyx-tube 2–2.5 mm. long, in anthesis 1–1.5 mm. broad, in fruit 2–2.5 mm. broad, glabrous or sparsely scaberulent; lobes 5–6, linear-lanceolate to linear-spatulate, obtuse or acutish, entire, 3–5 mm. long, about 1 mm. broad, glabrous; corolla infundibuliform, 7–8 mm. long, yellow; corolla-tube somewhat elongated, 2.5–3 mm. long, about 3 mm. broad at the orifice, sparsely pilose at the orifice within; lobes 5, elliptic-oblong, about 5 mm. long, about 2 mm. broad, obtuse; stamens slightly exserted, 5–6 mm. long; filaments glabrous, connective slightly prolonged at the

apex into a short cylindrical protuberance; pistil about 6 mm. long; ovules 4 in each cell; stigma capitate; capsule 5–6 mm. long, 10–11 mm. broad; seeds 4 in each cell, 5–5.5 mm. long, about 3 mm. broad, rather coarsely and regularly reticulated.

Distribution: Paraguay to central Argentina.

Specimens examined:

SOUTH AMERICA:

PARAGUAY: in campo humido in regione cursus superioris fluminis Apa, Dec. 1901–2, *Hassler 8278* (DC. herb. at Geneva, photograph, TYPE).

ARGENTINA: clay lowlands, General Roca and vicinity, Rio Negro Valley, alt. 250–360 m., Dec. 29, 1914, *Fischer 221* (US); vicinity of General Roca, Rio Negro, alt. 250–360 m., Sept. 1914–Feb. 1915, *Fischer 221* (F, G, M); en las lomas, Prov. de Tucuman, El Puestito, alt. 750 m., Nov. 14, 1928, *Venturi 7534* (G).

9. M. pinnatisecta Steyermark, n. sp.[39] Pl. 8, fig. 1.

An erect, nearly herbaceous perennial, 1–2 dm. high; stems fairly numerous, simple and somewhat elongated, slender, mostly terete, glabrous or rarely sparse-puberulent on the margins of the decurrent petioles; leaves opposite, numerous, crowded, shortly

[39] **M. pinnatisecta** Steyermark, sp. nov., erecta, subherbacea perennis, 1–2 dm. alta; caulibus plus minusve numerosis, simplicibus et subelongatis, angustis, teretibus plerumque, glabris vel infrequenter paulo puberulis; foliis oppositis, numerosis, congestis, breve petiolatis, anguste linearibus vel lineari-lanceolatis, petiolis includentibus, 4–20 mm. longis, alte pinnatisectis vel supremis integris, subcoriaceis, distincte cum nervo albo et margine albo, glabris, laciniis anguste linearibus vel lineari-lanceolatis, 3–13 mm. longis, 0.5–1.8 mm. latis, acutis vel acuminatis; floribus numerosis, cymis dichasialis subcorymbosis; pedicellis circiter 5 mm. longis, glabris, erectis in fructu; calyce anguste campanulato, 5–8 mm. longo, glabro vel sparse puberulo, calycis tubo 2.5–3 mm. longo, in florescente circiter 1.5 mm. lato, in fructu circiter 3.5 mm. lato; lobis 7–12, anguste linearibus, acutis vel acuminatis, integris, 3.5–6 mm. longis, 0.3–0.6 mm. latis; corolla subrotata, 7.5–10 mm. longa; corollae tubo brevi, 3 mm. longo, circiter 2 mm. lato orificio, ad apicem intra piloso; lobis 5–6, anguste elliptico-oblongis vel elliptico-lanceolatis, plus minusve acutis, mucronatis, 5–6 mm. longis, 1.75–2 mm. latis; staminibus paulo exsertis, circiter 6 mm. longis; filamentis glabris, connectivo elongato apice in protuberans relative longum cylindratum; polline plus minusve minute et regulariter reticulato (62.50); 68.75–81.25; (100.0) μ in diametro; pistillo circiter 7 mm. longo; ovulis 4 in quaque cella; stigmate capitato; capsula 5–6 mm. longa, circiter 10 mm. lata; seminibus 4 in quaque cella, rugose et regulari reticulato, 4–5 mm. longis, 3 mm. latis.—TYPE collected on el campo, Las Palmas, Territorio del Chaco, Argentina, Nov. 9, 1917, *Jörgensen 2643* (G).

petiolate, narrowly linear to linear-lanceolate, including the petiole, 4–20 mm. long, deeply pinnatisect or the uppermost entire, subcoriaceous, conspicuously white-nerved and white-margined, glabrous, the segments narrowly linear to linear-lanceolate, 3–13 mm. long, 0.5–1.8 mm. broad, acute to acuminate; flowers numerous, in dichasial subcorymbose cymes; pedicels about 5 mm. long, glabrous, erect in fruit; calyx narrowly campanulate, 5–8 mm. long, glabrous to sparsely puberulent; calyx-tube 2.5–3 mm. long, in anthesis about 1.5 mm. broad, in fruit about 3.5 mm. broad; lobes 7–12, narrowly linear, acute to acuminate, entire, 3.5–6 mm. long, 0.3–0.6 mm. broad; corolla subrotate, 7.5–10 mm. long; corolla-tube short, 3 mm. long, about 2 mm. broad at the orifice, pilose at the orifice within; lobes 5–6, narrowly elliptic-oblong to elliptic lanceolate, more or less acute, mucronate, 5–6 mm. long, 1.75–2 mm. broad; stamens slightly exserted, about 6 mm. long; filaments glabrous, connective prolonged at the apex into a relatively long, cylindrical protuberance; pollen grain finely and regularly reticulate, (62.50); 68.75–81.25; (100.0) μ in diameter; pistil about 7 mm. long; ovules 4 in each cell; stigma capitate; capsule 5–6 mm. long, about 10 mm. broad; seeds 4 in each cell, coarsely and irregularly reticulate, 4–5 mm. long, 3 mm. broad.

Distribution: northeastern Argentina.

In its 7–12 calyx-lobes and deeply pinnatisect leaves this species differs from its closest affinities, *M. integrifolia* var. *trifida* and *M. Hassleriana*. From the former it also differs in its more or less erect strict habit, and from the latter in its acute to acuminate leaf segments.

Specimens examined:

SOUTH AMERICA:

ARGENTINA: common on el campa, Las Palmas, Territorio del Chaco, Nov. 9, 1917, *Jörgensen 2643* (G TYPE).

10. M. scabra (Engelm.) A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Torrey in Pacif. R.R. Rept. **7**: 18. *pl. 7*. 1857; Walp. Ann. Bot. **5**: 487. 1858; A. Gray, Syn. Fl. N. Am. **2**[1]: 78. 1878; Rothrock in Rept. Wheeler Exp. 185. 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 384. 1881, and **4**: 67. 1886; Watson in Proc. Am. Acad. **18**:

112. 1883; Coulter in Contr. U. S. Nat. Herb. **2**: 261. 1892; Knobl. in Engler & Prantl, Nat. Pflanzenf. **4**²: 14. *fig. 8.* 1895; Small, Fl. S. E. U. S. ed. 1. 916. 1903, and ed. 2. 917. 1913; Wooton & Standley in Contr. U. S. Nat. Herb. **19**: 497. 1915; Rydb. Fl. Rocky Mts. 656. 1917, and ed. 2. 656. 1922; Standl. in Contr. U. S. Nat. Herb. **23**: 1138. 1924; Tidestrom in Contr. U. S. Nat. Herb. **25**: 413. 1925; Jepson, Man. Fl. Pl. Calif. 761. 1925. Pl. 4. figs. 13–14; pl. 7, fig. 2.

Bolivaria scabra Engelm. mss.

A nearly herbaceous, erect perennial, 0.7–3.5 dm. high, simulating species of *Linum* in appearance; stems numerous, slender, strict, mostly terete, clustered below, simple and elongated above, sparsely to moderately scaberulent or rarely glabrous, internodes short; leaves opposite or alternate, numerous, crowded, sessile, foliose throughout, linear to linear-lanceolate, the lowest mostly oblong-lanceolate to obovate, 8–38 mm. long, 1–4 mm. broad, entire, acute, subcoriaceous, sparsely hirtellous, especially on the margins and midrib; flowers very numerous, in dichasial to pleiochasial subcorymbose cymes; pedicels slender, 3–20 mm. long, sparsely scaberulent, erect in fruit; calyx campanulate, 4–9 mm. long, somewhat scaberulent; calyx-tube 1.5–3 mm. long, in anthesis 1.5–3 mm. broad, in fruit 3–5 mm. broad; lobes 7–12, equal or unequal, linear to linear-spatulate, entire, acute to slightly obtuse, 3–7 mm. long, 0.2–0.8 mm. broad, slightly roughened; corolla subrotate, 9–12 mm. long, bright yellow, corolla-tube short, 3–4 mm. long, 2–3 mm. broad at the orifice, pilose at the orifice within; lobes 5, oblong to obovate, obtuse, slightly mucronate, 5–8 mm. long, 3–5 mm. broad, glabrous or sparsely pilose without; stamens exserted, 6–8 mm. long; filaments glabrous, connective prolonged into a short rounded protuberance; pollen grain finely and regularly reticulate, 62.5–87.5; (100.6) μ in diameter; pistil usually 8–9 mm. (rarely 10–11 mm.) long; ovules 4 in each cell; stigma capitate; capsule 5–7 mm. long, 7–12 mm. broad; seeds 4 in each cell, scrobiculate (with small, narrow, deeper irregular pits), seeming smooth to the naked eye, 5–6 mm. long, 4 mm. broad.

Distribution: southern Colorado, Utah and Lower California, south to Durango, Mexico.

Specimens examined:

UNITED STATES:

TEXAS: El Paso, Aug. 4, 1920, *Schulz 221* (NY).

COLORADO: gravelly adobe soil in Pinon forest, along foothills, road 10 mi. n. of Canon City, between Canon City and Colorado Springs, July 3, 1921, *Bethel* (G); dry soil, open woods, east of Canon City, Fremont Co., alt. 1720 m., July 3, 1921, *Bethel, Willey & Clokey 4236* (F, M, NY, P, POM, US); Pueblo Co., Oct. 20, 1873, *Greene 8* (F); Betio, Canon City and Colorado Springs, June 30, 1927, *Osterhout 6840* (NY, POM).

NEW MEXICO: Pecos, alt. 2100 m., June 18, 1927, *Arsène 18616* (POM); La Glorieta, Sept. 1879, *T. S. Brandegee 11936* (M); Nutt, Sept. 3, 1903, *Diehl 750* (POM); Santa Fe, July 20, 1898, *Earle 74* (M, NY); wash near Paddy's hole, Catron Co., July 28, 1924, *Eggleston 20354* (NY); Sandia Mts., 1914, *Ellis 372* (US); open flats, eastern slope Las Palomas, Sandia Mts., alt. 2135 m., June 18, 1914, *Ellis 372* (NY, US); arid hills near Santa Fe, Sept. 8, 1881, *Engelmann* (M); 1847, *Fendler 693* (C, F, G, M, NY, P, US); Albuquerque, *Harward* (M); Santa Fe, alt. 2195 m., July 8, 1897, *A. A. Heller & E. G. Heller 3826* (G, M, NY, POM, US); Monument No. 40, Mexican boundary line, May 9, 1892, *Mearns 252* (US); Pinus Altus, Aug. 9, 1895, *Mulford 807* (US); Pinus Altus, Aug. 7, 1895, *Mulford 805* (NY); between Anton Chico and Las Vegas, Oct. 1, 1913, *Rose & Fitch 17653* (NY, US); Santa Fe, June, 1874, *Rothrock 60* (F, P); plains, near Ft. Wingate, July, 1880, *Rusby 255* (C, F, M, NY, US); 1881, *Rusby* (NY); cedar slopes, near Queen, Aug. 12–20, 1924, *Standley 40689* (US); dry hillside near Carlsbad Cavern, Aug. 12–20, 1924, *Standley 40400* (US); dry field, Black River, Eddy Co., Aug. 12–20, 1924, *Standley 40455* (US); dry rocky slope, near Sitting Bull Falls, Guadalupe Mts., Aug. 12–20, 1924, *Standley 40729* (US); near Pecos, San Miguel Co., alt. 2042 m., Aug. 15, 1908, *Standley 4967* (G, M, NY, US); *Thurber 693* (G); n. hillside, High Rolls and vicinity, Otero Co., alt. 1830 m., May 21–28, 1902, *Viereck 500251* (P); Ojo del Muerto, south of Santa Fe, Aug. 2, 1846, *Wislizenus 68* (M TYPE); 5 mi. west of Silver City, July 4, 1906, *Wooton* (US); 1851–52, *Wright 1694* (US).

ARIZONA: rim, Grand Canyon, July 6, 1912, *Condit* (C); Duncan

Plains, Oct. 1, 1900, *Davidson 444a* (G); Blue River, Sept. 10, 1902, *Davidson 756* (POM); moist cañon, July 21, 1896, *Fernow* (US); semi-meadow, 12 miles n. of White River, White Mts., alt. 1616.5 m., June 23, 1930, *Goodman & Hitchcock 1302* (M); Ash Fork, June 20, 1903, *Griffiths 4767* (US); Prescott, July 8–25, 1903, *Griffiths 4882* (US); White Mts., Aug. 6–15, 1903, *Griffiths 5389* (US); along road to Hopi Point, Grand Canyon, alt. 1500–2100 m., July 1, 1913, *Hitchcock 104* (US); Ft. Apache, July 10, 1901, *M. Z. Hough* (F); Chalcedony Park, July, 1897, *W. Hough 34* (G, M, US); Phoenix, alt. 350 m., May 6, 1903, *M. E. Jones* (POM); Clemenceau, May 25, 1922, *W. W. Jones* (M); Cedar Glade, June 16, 1922, *W. W. Jones* (M); near Flagstaff, alt. 610 m., June 23, 1901, *Leiberg 5555* (US); Santa Catalina Mts., May, 1881, *Lemmon 164* (C); Ft. Lowell, *Lemmon* (C); in the vicinity of Flagstaff, alt. 2133 m., July 4, 1898, *MacDougal 218* (C, F, G, NY, P, US); Fort Apache, 1901, *Mayerhoff 105*, in part (F); 1869, *Ed. Palmer* (P, US); rocky soil, Flagstaff, May–Oct., 1900, *Purpus 8057* (C, M, POM, US); Peach Springs, July 6, 1883, *Rusby 718* (M); 10 mi. s. of Grand Canyon, July 13, 1892, *Wooton* (US); Holbrook, Aug. 17, 1896, *Zuck* (US); Prescott, July 29, 1896, *Zuck* (NY).

UTAH: southern Utah, 1877, *Ed. Palmer 65* (G, M, NY, US); rocky soil, Cane Spring Mts., alt. 1220–1525 m., May–Oct., 1898, *Purpus 6228* (C, NY, US).

MEXICO:

LOWER CALIFORNIA: July 4, 1884, *Orcutt* (US); Cantillas Mts., July, 1884, *Orcutt* (US); Japa, July 25, 1883, *Orcutt 926* (C); Parry's Pinesap, April 7, 1884, *Orcutt* (C, F).

CHIHUAHUA: Ojo de Vaca, etc., June, 1851, *Thurber 318* (F, G); Copper Mines, July, 1851, *Thurber 232* (G, NY).

DURANGO: Tepehuanes, June 4–25, 1906, *Ed. Palmer 309* (C, F, NY, US).

10a. Var. **laevis** (Wooton & Standley) Steyermark, n. comb.

M. laevis Wooton & Standley in Contr. U. S. Nat. Herb. [Fl. N. Mex.] **16**: 158. 1913, and **19**: 497. 1915.

Leaves, including the petiole, 2–17 mm. long, 1–5 mm. broad, obtuse or acute, distinctly mucronate, glabrous or sparsely

scaberulent, the lower and middle ones ovate or elliptic-oblong to oblong-lanceolate, the upper ones becoming lanceolate; pedicels glabrous to moderately scaberulent; calyx glabrous to slightly roughened; corolla 11–14 mm. long; corolla-tube almost entirely glabrous within except for the few slender hairs around the insertion of the filament on the tube; lobes elliptic-obovate to subovate, acute to acuminate, distinctly mucronate; connective of the anther prolonged at the apex into a short subcuneate protuberance; seeds 4–5 mm. long, 3–3.5 mm. broad.

Distribution: southwestern Texas, west to southeastern California and Mexico.

Specimens examined:

UNITED STATES:

TEXAS: semi-desert, mountain sides, Franklin Mts., near El Paso, Altura Park, El Paso Co., July 10, 1911, *Barlow* (F); Mesa, El Paso, May 8–19, 1902, *Earle 482* (NY); common and abundant, rocky slopes and along dry creek beds, Redford, Aug. 7, 1919, *Hanson 791* (US); common and abundant along arroyos and slopes, Redford, Aug. 7, 1919, *Hanson 791* (G); El Paso, June 4, 1895, *Mulford 251* (M, NY); near Medira Creek, Presidio Co., Sept., 1892, *Nealley 159a* (US); Langtry, Valverde Co., May, 1913, *Orcutt 6131* (POM); rocky banks, along Blue Creek, near Trap Mountain, Chisos Mountains, Brewster Co., May 26, 1928, *E. J. Palmer 34191* (M TYPE); El Paso, Aug. 1920, *Schulz 247* (POM); El Paso, Aug. 4, 1920, *Schulz 221* (NY); vicinity of El Paso, Sept., 1911, *Stearns* (US); mesas, vicinity of El Paso, 1911, *Stearns 66* (US); vicinity of El Paso, 1911, *Stearns* (NY); hills bordering salt basin, west of Kent, Aug. 6, 1916, *Young* (M).

NEW MEXICO: Socorro, July 14, 1897, *Herrick* (US); Socorro, July 14, 1897, *Herrick 708* (US); Rincon, Sept. 9, 1884, *M. E. Jones 4167* (F, NY, US); Cedar Spring, Aug. 27, 1895, *Mulford 1073* (US); Mexican Boundary Survey, *Parry, Bigelow & Schott* (NY); Organ Mts., 1881, *Vasey* (F, G, US TYPE of *M. laevis*); 1881, *Vasey* (NY); Monument No. 6 to Monument No. 12, Sept. 20–24, 1892, International Boundary Commission U. S. & Mexico, *Wagner 956* (US); Organ Mountains, Dona Ana Co., alt. 1433.5 m., July 15, 1897, *Wooton 154* (C, G, M, POM, US); La Luz Canyon, Sacramento Mts., Aug. 27, 1901, *Wooton* (US); on the

mesa west of the Organ Mountains, Little Mt., Dona Ana Co., Aug. 29, 1903, *Wooton* (M); on the mesa west of the Organ Mts., Dona Ana Co., Aug. 29, 1902, *Wooton* (C, POM); in the Organ Mts., Dona Ana Co., alt. 1677.5 m., Sept. 23, 1906, *Wooton & Standley* (US); 1851–52, *Wright 1694* (NY, US).

ARIZONA: eight mi. s. of Vail, alt. 1220 m., Aug. 31, 1903, *M. E. Jones* (POM); mesas, Tucson, alt. 732 m., May 22, 1903, *Thornber 448* (C, M, NY, POM, US); mesas, Tucson, Aug. 27, 1901, *Thornber* (C).

CALIFORNIA: Barnwell, May, 1911, *K. Brandegee* (C).

MEXICO:

CHIHUAHUA: hills near Chihuahua, Aug. 9, 1885, *Pringle 549* (G); abundant on mesas, Oct. 1911, *Stearns 66* (F, G).

10b. Var. **ramosissima** Steyermark, n. var.[40]

A paniculately branched, erect, suffruticose perennial, 3–9 dm. high, not simulating species of *Linum* in appearance; stems much branched, but not clustered below; internodes elongated, petiolate below, subsessile above, elliptic-oblong to sublanceolate, including the petiole, 5–40 mm. long, 1–9 mm. broad, submembranaceous, distinctly mucronate, glabrous to sparsely scaberulent; flowers in loose pleiochasial paniculate to subcorymbose cymes; calyx glabrous to densely scaberulent; corolla-tube 4.5–5 mm. long; corolla-lobe 4.5–6 mm. long; stamens 9–10 mm. long; connective prolonged at the apex into a short, cylindrical, blunt protuberance; pistil 10–11 mm. long; seeds coarsely reticulate with the deeper irregular pits appearing on the surface more frequently than in the species, 4.5–5 mm. long, about 3 mm. broad.

Distribution: western Texas to central Arizona and northern Mexico.

[40] Var. **ramosissima** Steyermark, var. nov., paniculate ramosa, erecta, suffruticosa perennis, 3–9 dm. alta, non simulans speciebus Lini habitu; caulibus multo ramosis, sed non congestis infra; internodiis elongatis, inferioribus petiolatis, superioribus subsessilibus, elliptico-oblongis, 5–40 mm. longis, 1–9 mm. latis, submembranaceis, distincte mucronatis, glabris vel sparse scaberulentis; floribus pleiochasialis paniculatis vel subcorymbosis in cymis; corollae tubo 4.5–5 mm. longo; corollae lobis 4.5–6 mm. longis; staminibus 9–10 mm. longis, connectivo elongato apice in protuberans breve cylindratum; pistillo 10–11 mm. longo; seminibus reticulatis cum plus rugositate, cum cavibus altioribus occurrentibus plus frequenter in integumento exteriore quam in specie, 4.5–5 mm. longis, circiter 3 mm. latis.—TYPE collected near El Paso, El Paso Co., Texas, June 19, 1926, *E. J. Palmer 31083* (M).

Specimens examined:

UNITED STATES:

TEXAS: El Paso, Sept. 22, 1901, *Bailey 748* (US); common in gulches, eastern slope Franklin Mts., El Paso Co., June 29, 1921, *Ferris & Duncan* (M, NY); El Paso, July 17, 1922, *Fisher 319* (NY); Chenates region, 1889, *Nealley 471* (F, US); dry rocky ground, near El Paso, El Paso Co., June 19, 1926, *E. J. Palmer 31083* (M TYPE); Franklin Mts., El Paso Co., Sept. 1915, *Slater* (US); gravelly mesa, west side of Chisos Mts., Brewster Co., June 27, 1931, *Moore & Steyermark 3256* (G, M, NY); western Texas, *Wright* (P); foothills of Chenate Mts., Sept. 9, 1914, *Young 54* (M); foothills of Chenate Mts., Sept. 8, 1914, *Young 11* (M); foothills of Chenate Mts., Sept. 9, 1914, *Young* (M).

NEW MEXICO: on hillsides, Lake Valley, Sept. 1914, *Beals* (US); Mexican Boundary Survey, in the valley of Rio Grande, below Donana, *Bigelow* (NY); Albuquerque, Sept. 4, 1894, *Herrick* (NY); Rincon, Sept. 9, 1884, *M. E. Jones 4167* (POM); near mouth dry cañon in arroyo, Alamogordo, Otero Co., alt. 1403 m., April 7–May 24, 1902, *Rehn & Viereck 500249* (P); to arroyo base foothills, Alamogordo, Otero Co., alt. 1326.75 m., April 7–May 24, 1902, *Rehn & Viereck 500250* (P); Tortugas Mts., e. of Mesilla Park, July 15, 1906, *Standley 545* (M); Monument No. 6 to Monument No. 12, Sept. 20–24, 1892, International Boundary Commission U. S. & Mexico, *Wagner 956* (US); Little Mt., near Las Cruces, alt. 1220 m., Sept. 2, 1894, *Wooton* (NY); Organ Mts., Dona Ana Co., alt. 1433.5 m., July 15, 1897, *Wooton 154* (NY); on the mesa west of the Organ Mts., Tortugas Mts., Dona Ana Co., alt. 1281 m., Sept. 1, 1908, *Wooton & Standley* (US); on the mesa west of the Organ Mts., Tortugas Mts., Dona Ana Co., alt. 1403 m., Aug. 19, 1906, *Wooton & Standley* (US); on the mesa west of the White Mts., Tortugas Mt., Lincoln Co., July, 1906, *Wooton & Standley* (US); May–Oct. 1849, *Wright 563* (F, G, NY, US); 1851–52, *Wright 1694* (F, G, NY).

ARIZONA: Roosevelt Dam, May 17, 1919, *Eastwood 8671* (G, US); buttes, Tempe, April 21, 1892, *Ganong & Blaschka* (G); on "prairie," N. Fifth Ave., vicinity of Tucson, April 29, 1913, *J. M. & M. T. Greenman 4a* (M); Tucson Mountain, vicinity of Tucson, alt. 762.5 m., April 11, 1913, *J. M. & M. T. Greenman 4*

(M); on trip to Tucson Mt., March 7, 1901, *Griffiths 2436* (NY); Ft. Apache, 1893, *Hoyt* (NY); Tucson, alt. 701.5 m., Aug. 17, 1903, *M. E. Jones* (POM); Congress Junction, alt. 915 m., May 1, 1903, *M. E. Jones* (M, POM, US); Papago Reservation, May 7, 1930, *M. E. Jones 26448* (M); desert, Phoenix, May 18, 1897, *Kunze* (NY); Santa Catalina Mts., May, 1881, *Lemmon 164* (C); Sierritas Mts., west of Tucson, April, 1881, *Lemmon 164* (G); Dutch Charley's Ranch, near Monument No. 88, Mexican Boundary Survey, Aug. 13, 1893, *Mearns 1868* (NY, US); Camp Grant, May 4, 1867, *Ed. Palmer 206* (G); on the mesas at Camp Grant, May 4, 1867, *Ed. Palmer 206* (M); Lowell and Tucson, April–May, 1884, *W. F. Parish 142* (F); Nogales, Aug. 28, 1927, *Peebles & Harrison 4725* (US); hills near Tucson, April 27, May 17, 1883, *Pringle* (F, G, NY, P, US); hills near Tucson, May, 1883, *Pringle 15602* (M); Bradshaw Mt., alt. 2836.5 m., April–Sept., 1903, *Purpus* (C); Desert Botanical Laboratory, Tucson, 1905, *Rose 44* (US); laboratory hill, in vicinity of Tucson, April 27, 1910, *Rose, Standley & Russell 15188* (US); Sienega, alt. 1183.4 m., Aug., 1874, *Rothrock 561* (F, G, US); Tumamoc Hill, alt. 793 m., Aug., 1916, *Shreve 4896* (AR); Tucson, Tumamoc Hill, alt. 793 m., Sept. 20, 1916, *Shreve 4988* (C); Tucson, May 15, 1892, *Toumey 206a* (US); Copper town?, Aug. 25, 1894, *Toumey* (NY); Holbrook, Aug. 17, 1896, *Zuck* (US).

MEXICO:

NUEVO LEON: Monterey, *Eaton & Edwards* (NY).

CHIHUAHUA: Sabinal, Sierra Madre Mts., alt. 1281 m., Sept. 29, 1903, *M. E. Jones* (POM); between Casas Grandes and Sabinal, Sept. 4–5, 1899, *Nelson 6362* (US); common on mesas, Oct. 1911, *Stearns* (F); Santa Eulalia hills, Aug. 8, 1885, *E. Wilkinson* (C); St. Eulalia Mts., May 29, 1885, *Wilkinson* (F, US).

10c. Var. longituba Steyermark, n. var.[41]

Internodes elongated; leaves not crowded, mostly remote,

[41] Var. **longituba** Steyermark, var. nov., internodiis elongatis; foliis non congestis, plerumque remotis oblanceolatis vel lanceolatis, 1.5–7 mm. latis, submembranaceis, glabris; floribus in laxis paniculatis cymis; corolla infundibuliforme, 15–17 mm. longa, corollae tubo relative elongato, 6–7 mm. longo, 4–4.5 mm. lato orificio; lobis 9–10 mm. longis, 5–6 mm. latis, distincte mucronatis, staminibus 10–12 mm. longis; pistillo 13–14 mm. longo.—TYPE collected in the Massatzal Mountains, May 5, 1867, *Smart 213* (G).

oblanceolate to lanceolate, 1.5–7 mm. broad, submembranaceous, glabrous; flowers in loose paniculate cymes; corolla infundibuliform, 15–17 mm. long, corolla-tube relatively elongated, 6–7 mm. long, 4–4.5 mm. broad at the orifice; lobes 9–10 mm. long, 5–6 mm. broad; stamens 10–12 mm. long; pistil 13–14 mm. long.

Distribution: central Arizona.

Specimens examined:

ARIZONA: Massatzal Mountains, May 5, 1867, *Smart 213* (G TYPE).

11. M. decemfida (Gill.) A. Gray in Am. Jour. Sci. II. **14**: 44. 1852; Walp. Ann. Bot. **5**: 487. 1858; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881. Pl. 8, fig. 2.

Bolivaria decemfida Gill. ex Hook. & Arn. in Hook. Jour. Bot. **1**: 284. 1834; A. DC. in DC. Prodr. **8**: 315. 1844.

A small, erect, branching, suffruticose perennial, simulating *Spartium radiatum* in appearance; stems rather numerous, slender, strict, 4-angled, glabrous; leaves not crowded, opposite, sessile, linear-lanceolate, 5–15 mm. long, 1–2 mm. broad, entire, acute, glabrous, subcoriaceous; flowers numerous in dichasial cymes; pedicels slender, 3–5 mm. long, 0.5–0.8 mm. broad, glabrous; calyx campanulate, 5–7 mm. long, glabrous, calyx-tube 3–3.5 mm. long, about 2 mm. broad in anthesis; lobes entire, about 10, linear, 2–3 mm. long, about 0.2 mm. broad, acute to acuminate; corolla shortly infundibuliform, 13–16 mm. long, corolla-tube about 6 mm. long, about 3 mm. broad at the orifice, densely pilose within; lobes 5, narrowly oblong, obtusish or mucronate, 7–11 mm. long, 3–4 mm. broad; stamens exserted, 15–16 mm. long; filaments glabrous, connective slightly prolonged at the apex into a blunt, cylindrical protuberance; pollen grain finely and regularly reticulate, (56.25); 62.50–71.25 (76.25) μ in diameter; pistil 10–13 mm. long; ovules 4 in each cell; stigma capitate; capsule not seen.

Distribution: valleys of the Andes of Mendoza, central Chile.

The specimen cited is the only one so far encountered which agrees with the original description.

Specimens examined:

SOUTH AMERICA: with incomplete data, *Fielding* (G), "collector *Gillies* in Fielding Herbarium," according to I. M. Johnston.

11a. Var. longifolia Steyermark, n. var.[42]

Leaves, including the petiole, 6–40 mm. long, slightly mucronate; calyx 5–11 mm. long, calyx-tube 2–3 mm. long; lobes 8–11, 4–8 mm. long; corolla-tube 4–5 mm. long; corolla-lobes oblong to obovate, 10–12 mm. long, 5–8 mm. broad; stamens 11–12 mm. long.

Distribution: central Mexico and Texas.

This is here treated as a variety of the South American *M. decemfida*, which it resembles very closely. One might expect that the geographical distribution of a species and its variety would more nearly approach each other than is found in this case. However, notwithstanding the fact that, as far as present collections are concerned, the species and its variety are geographically widely separated, yet the close morphological relationships between the two seem to warrant the tentative treatment of the Texas and Mexican plant as a variety of the Chilean species.

Specimens examined:

UNITED STATES:

TEXAS: foothills of Chisos Mts., July, 1883, *Havard* (US); gravelly mesa, west side of Chisos Mts., Brewster Co., June 27, 1931, *Moore & Steyermark 3257* (C, M, NY).

MEXICO:

SAN LUIS POTOSI: 1879, *Schaffner 506* (F); Sept., 1876, *Schaffner 67* (G).

DURANGO: Santiago Papasquiara, April, Aug. 1896, *Ed. Palmer 429* (C, F, M TYPE, NY, US).

12. M. longiflora (Engelm.) A. Gray in Am. Jour. Sci. II. **14**: 45. 1852; Walp. Ann. Bot. **5**: 488. 1858; A. Gray, Syn. Fl. N. Am. **2**[1]: 78. 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881, and **4**: 67. 1886; S. Watson in Proc. Am. Acad. **18**: 122. 1883; Coulter in Contr. U. S. Nat. Herb. **2**: 268. 1892; Knobl. in Engler & Prantl, Nat. Pflanzenf. **4**[2]: 14. 1895; Standl. in Contr. U. S. Nat. Herb. **23**: 1137. 1924. Pl. 4, fig. 4; pl. 9, fig. 1.

[42] Var. longifolia Steyermark, var. nov., foliis, petiolis includentibus, 6–40 mm. longis, submucronatis; calyce 5–11 mm. longo; calycis tubo 2–3 mm. longo; lobis 8–11, 4–8 mm. longis; corollae tubo 4–5 mm. longo; corollae lobis oblongis vel obovatis, 10–12 mm. longis, 5–8 mm. latis; staminibus 11–12 mm. longis.—TYPE collected at Santiago Papasquiara, state of Durango, Mexico, April, August, 1896, *Ed. Palmer 429* (M).

M. pubens A. Gray in Am. Jour. Sci. II. **14**: 45. 1852; A. Gray, Syn. Fl. N. Am. 2^1: 79. 1878; S. Watson in Proc. Am. Acad. **18**: 112. 1883; Coulter in Contr. U. S. Nat. Herb. **2**: 261. 1892; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^3: 14. 1895.

Menodoropsis longiflora (A. Gray) Small, Fl. S. E. U. S. ed. 1, 917. 1903, and ed. 2, 917. 1913.

Menodora hispida Palmer in Jour. Arnold Arb. **10**: 43. 1929.

Bolivaria longiflora Engelm. mss.

An erect, branching, nearly herbaceous perennial, 1–9 dm. high; stems very numerous, slender, almost simple, and much elongated, to paniculately branched and shortened, slightly angled, glabrous to densely hirsute-pilose; internodes short, leaves mostly opposite or the uppermost alternate, numerous, sessile to subpetiolate, linear to elliptic-lanceolate, or elliptic-oblong, 5–55 mm. long, 2–8 mm. broad, mostly entire, occasionally the lowest bi- or tri-lobed, obtuse to acute or mucronate, glabrous to somewhat hirsute-pilose, subcoriaceous; flowers numerous in terminal subcorymbose cymes; pedicels slender, 5–22 mm. long, glabrous to moderately hirsute-pilose, erect in fruit; calyx campanulate to turbinate, 8–23 mm. long, glabrous to somewhat hirsute-pilose; calyx-tube 2–3 mm. long, in anthesis 2–3 mm. broad, in fruit 4–6 mm. broad; lobes 8–12, mostly 10, equal or unequal, linear, entire and rarely bifid, 8–18 mm. long, 0.2–1 mm. broad, glabrous to moderately hirsute; corolla hypercrateriform, 30–60 mm. long, bright yellow, corolla-tube 25–53 mm. long, 4–5 mm. broad at the orifice, entirely glabrous; lobes 5, ovate, acute, distinctly mucronate, 9–15 mm. long, 5–8 mm. broad; stamens included; filaments glabrous; pollen grain with more or less regular reticulation, (112.55); 125–143.75; (162.5) μ in diameter; pistil 25–50 mm. long; ovules 4 in each cell; stigma broadly capitate; capsule 8–10 mm. long, 10–17 mm. broad; seeds 4 in each cell, with large irregular reticulations, 5–7 mm. long, 4–5 mm. broad.

Distribution: western Texas and southern New Mexico south to the state of Puebla, Mexico.

The plant which E. J. Palmer recently described as a new species, namely, *M. hispida*, is in all respects like *M. longiflora*. The numerous and very elongated calyx-lobes and the large capsule place it at once with the latter species. Although Palmer

states at the end of his description, "flowers not seen," the writer nevertheless has found one or two flowers on the specimen which were badly aborted by insects. Because of this insect injury there are no fully developed flowers on the specimen, but the remains of the long, hypercrateriform corolla, which is characteristic of no other species except *M. longiflora*, is slightly indicated.

The writer has also found it necessary to treat Gray's *Menodora pubens* as synonymous with *M. longiflora*, since numerous specimens have been found which show intergradations in the degree of pubescence and breadth of the leaves. Gray describes *M. pubens* as "pubescent throughout with soft and spreading hairs: leaves rather broader: otherwise nearly resembling the preceding." Since so much intergradation occurs in the degree of pubescence and in the breadth of the leaves, and since no other morphological characters have been found which will distinguish the glabrous from the pubescent forms, it has been thought better to treat such examples under one species.

Specimens examined:

UNITED STATES:

NEW MEXICO: on ridge at head of Willow Seep Canyon, Guadalupe Mts., Lincoln (Alamo) Forest, alt. 2165 m., Sept. 14, 1916, *Chapline 485½* (NY); in the valley of the Rio Grande, below Donana, *Parry, Bigelow, Wright & Schott 1100* (NY); Queen, alt. 1799.5 m., Aug. 2, 1909, *Wooton* (US); vicinity of Queen, Eddy Co., Aug. 1, 1909, *Wooton* (US).

TEXAS: *Bigelow 80* (F); Glass Mts., Sept. 10, 1925, *Bogusch 984* (POM); *Buckley* (P); scattered, woodland, ridge 1 mi. s. of McCollaum's Ranch, Lincoln (Alamo) Forest, alt. 2135 m., Oct. 3, 1915, *Chapline 485* (G); rocks in canyon, North Van Horn, El Paso Co., July 8, 1900, *Eggert* (G, M); between Sonora and "Swayer Spring" at head of Llano River, Sutton Co., alt. 700 m., July 16, 1920, *Eggleston 16725* (US); chaparral slopes, Juniper Cañon, Chisos Mts., Brewster Co., alt. 1680 m., July 15–18, 1921, *Ferris & Duncan 2820* (M, NY); foothills of Chisos Mts., July, 1883, *Havard* (US); Kerrville, Kerr Co., alt. 488–610 m., June 12–19, 1894, *Heller 1880* (C, F, G, M, NY, POM, US); Kerrville, July, 1889, *Hopkins* (US); 1849–51, Pierdanales, *Lindheimer* (NY); upper Guadaloupe, June-July, 1847, *Lindheimer 652a* and *652b*

(M); on grassy, gravelly soil with *Dasylirion*, on the upper Guadaloupe, July, 1847, *Lindheimer 652* (F, G, M, US); Comanche Spring, New Braunfels, July, 1849, *Lindheimer 983* (F, G, M, NY, US); high plateaus on the upper Guadaloupe, sparsely on sterile gravelly soil, June, 1847, *Lindheimer 652* (M TYPE); on gravelly sterile soil, sparse, forming large bushes, with *Ruta*, *Dasylirion*, upper Guadaloupe, June–July, 1847, *Lindheimer 426* (G); Camp Charlotte, 1889, *Nealley 683*, and *684* (US); Camp Charlotte, 1889, *Nealley 294* (F); Chenates region, 1889, *Nealley 471a* (US); 1887, *Nealley* (US); western Texas, 1890, *Nealley* (F); dry rocky hillsides, Kerrville, Kerr Co., Oct. 2, 1916, *E. J. Palmer 10883* (M); dry limestone hills, Montell, Uvalde Co., Oct. 14, 1917, *E. J. Palmer 12976* (M); dry limestone hills, Montell, Uvalde Co., Oct. 15, 1917, *E. J. Palmer 12992* (M); rocky hillsides, Telegraph, Kimble Co., Oct. 8, 1916, *E. J. Palmer 10937* (M); rocky bluffs, Twin Mts., May 20, 1903, *Reverchon* (M); sandy soils, Sabinal, June, 1884, *Reverchon 1556* (M); rocky bluffs, Sabinal, Uvalde Co., June, 1885, *Reverchon 1556* (F, US); Rio Bravo del Norte, Springhills, Coalsprings, Aug. 1852, *Schott* (F); rocky grassy slope, upper Blue Creek, Chisos Mts., Brewster Co., June 25, 1931, *Moore & Steyermark 3242* (G, M, NY); dry rocky grassy flat, Lower McKittrick Canyon, Guadalupe Mts., Culberson Co., July 23, 1931 *Moore & Steyermark 3598* (G, M, NY); 1851–52, *Wright 1695* (F, G, NY), and *1696* (G, M, NY, US); May–Oct., 1849, *Wright 564* (C, F, G, NY, P, US); 1851, *Wright 248* (G); western Texas, *Wright 11935* (M); Rio Grande, 1848, *Wright* (G); lower slopes of Guadaloupe Mts., Aug. 28, 1916, *Young* (G, M); Davis Mts., Aug. 8, 1914, *Young* (M).

MEXICO:

NUEVO LEON: Monterrey, Sta. Catarina, La Fama, alt. 680 m., July, 1911, *Arsène & Abbon 6148* (M, NY, US).

COAHUILA: Saltillo, 1898, *Ed. Palmer 118* (C, F, NY, US); mountains north of Monclova, Feb.–Oct., 1880, *Ed. Palmer 792* (US); Juarez, Feb.–Oct., 1880, *Ed. Palmer 794* (US); mountains 24 mi. n. e. by n. from Monclova, first six days of September, 1880, *Ed. Palmer 792* (G, P); Juarez, about 100 miles north from Monclova, on the Sabinas River, Sept. 23–24, 1880, *Ed. Palmer 794* (F, G); near Parras, Oct., 1910, *Purpus 5004* (C, G); Sierra de Parras Oct. 1910, *Purpus 5022* (F, M, NY, US).

CHIHUAHUA: Santa Eulalia Mts., Sept. 26, 1885, *Pringle 539* (M).

PUEBLA: Acatzingo, Feb. 1, 1902, *Arsène 10* (F).

WITHOUT STATE: San Luis Potosi to San Antonio, Aug. 1878, *Parry* (P).

13. M. scoparia Engelm. ex A. Gray in Bot. Calif. **1**: 471. 1876; A. Gray, Syn. Fl. N. Am. **2**[1]: 78. 1878; Rothrock in Rept. Wheeler Exp. 185. 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 304. 1881; Knobl. in Engler & Prantl, Nat. Pflanzenf. **4**[2]: 14. 1895; Standl. in Contr. U. S. Nat. Herb. **23**: 1137. 1924; Jepson, Man. Fl. Pl. Calif. 761. 1925; Tidestrom in Contr. U. S. Nat. Herb. **25**: 413. 1925. Pl. 4, figs. 9–10.

M. scabra var. *glabrescens* Gray in Watson, Cat. Pl. Wheeler Exp. 15. 1874.

A paniculately branching, erect, suffruticose perennial, 3.5–9 dm. high; stems very numerous, much branched, opposite or clustered at the base, simple and elongated above, strict, slender, slightly angled, mostly glabrous or less often scaberulent; internodes elongated above; leaves opposite below, subalternate above, relatively few, including the petiole, 1–30 mm. long, 1–4 mm. broad, acute to obtusish, entire, mostly glabrous or sparsely scaberulent on the margins and upper surface, the lower slightly crowded, well developed, subpetiolate, oblong-obovate to oblanceolate, the upper remote, rudimentary, subsessile, linear or linear-subulate; flowers few, disposed in loose pleiochasial subcorymbose cymes; pedicels slender, 3–10 mm. long, glabrous or sparsely scaberulent, erect in fruit; calyx campanulate, 3–6 mm. long, glabrous or sparsely scaberulent; calyx-tube 1.5–2.25 mm. long, in anthesis about 2 mm. broad, in fruit about 4 mm. broad, mostly glabrous, rarely sparsely scaberulent; lobes usually 5–6 (infrequently with intermediate, smaller and narrower lobes, making 7, 8, or 10), linear to lanceolate, 1.5–4 mm. long, 0.5–1 mm. broad, acute to acuminate, entire, mostly glabrous, infrequently sparsely scaberulent on the margins; corolla subrotate, usually 9–10 mm. (sometimes 12–13 mm.) long, yellow; corolla-tube short, 3–5 mm. long, about 3 mm. broad at the orifice, moderately pilose at the orifice within; lobes 5, obovate, more or

less obtuse, 5–8 mm. long, 3–4 mm. broad; stamens slightly exserted, 7–9 mm. long; connective slightly prolonged into a blunt, cylindrical protuberance; pollen grain finely and irregularly reticulate, 75–87.5 μ in diameter; pistil 7–10 mm. (rarely 12–13 mm.) long; ovules 4 in each cell; stigma capitate; capsule 4–6 mm. long, about 10 mm. broad; seeds 4 in each cell, rather coarsely and regularly reticulate, 4–5 mm. long, about 3 mm. broad.

Distribution: Arizona to southeastern California and Lower California, south to Coahuila and Nuevo Leon, Mexico.

Specimens examined:

UNITED STATES:

ARIZONA: Skull Valley, Fort Whipple, June 4, 1865, *Coues & Ed. Palmer 223* (M); Pinery Creek, Chiricahua Mts., Aug., 1896, *Fernow* (US); steep slopes, Roosevelt Dam, Aug. 3, 1911, *Goodding 720* (G, NY); Yucca, May 14, 1884, *M. E. Jones* (POM); Yucca, May 17, 1884, *M. E. Jones 3924* (NY, POM, US); above Cornville, Aug. 20, 1921, *W. W. Jones* (M); Prescott, July 17, 1927, *Peebles, Harrison & Kearney 4261* (US); Peach Springs, July 6, 1883, *Rusby* (F, M, NY, P); stones and gravel, Peach Springs, 1883, *Rusby 266* (G); Prescott, Aug. 24, 1894, *Toumey* (C); Payson, June 23, 1892, *Toumey 206b* (US); 1874, *Wheeler* (G); 20 mi. from Kingman, May 20, 1893, *Wilson* (C, US); Prescott, July 31, 1911, *Wooton* (US).

CALIFORNIA: hills at Jacumba near the monument, San Diego Co., May 29, 1903, *Abrams 3641* (NY); dry gravelly hills, Jacumba, San Diego Co., May 29, 1903, *Abrams 3641* (C, G, M, NY, P, POM, US); Providence Mts., June 6, 1902, *T. S. Brandegee* (C); *Cooper* (US); at Fort Mojave, 1860–61, *Cooper* (G); dry hillsides, Jacumba, San Diego Co., alt. 854 m., May 22, 1924, *Fendge 557* (POM); rocky slopes, Providence Mts., alt. 1525 m., May 15, 1930, *Hoffmann* (St. B.); dry hills, Jacumba, San Diego Co., Aug. 13, 1917, *Munz 1683* (POM); dry slopes at base of mts., vicinity of Bonanza King Mine, east slope Providence Mts., Mojave Desert, May 21–24, 1920, *Munz, Johnston & Harwood 4264* (POM, US); San Diego Co., 1875, *Ed. Palmer* (G); San Diego Co., June, 1880, *S. B. & W. F. Parish 435* (M); Sorkin's Station, San Diego Co., June, 1880, *S. B. & W. F. Parish 435* (P); San Felipe, San Diego Co., June, 1882, *S. B. & W. F. Parish*

435 (F, NY); New York Mts., near Leastalk, San Bernardino Co., June 3, 1915, *S. B. Parish 10260* (C).

MEXICO:

LOWER CALIFORNIA: Las Huevitas, May 19, 1889, *T. S. Brandegee* (C); Agua Dulce, May 16, 1889, *T. S. Brandegee* (C); San Julio Cañon, April 20, 1889, *T. S. Brandegee* (F, G); El Rancho Viejo, April 24, 1889, *T. S. Brandegee* (P, US); Jacumba, alt. 854 m., July 9, 1922, *Fisher 36* (US); Cañon Cantillas, July 7, 1884, *Orcutt* (F); Cantillas Cañon, Aug. 1, 1883, *Orcutt* (C); Cantillas Mts., Aug. 1, 1883, *Orcutt 949* (G); Colton, June, 1880, *Vasey 362* (F, US).

COAHUILA: San Matias Pass, north end of San Pedro Martir Mts., alt. 915 m., June 28, 1905, *Goldman 1181* (US); on mountains, about Saltillo, Sept. 1848, *Gregg 527* (G, M TYPE), and Merilla, 1848–49, *Gregg 527* (NY); on mountains at La Azufrora, near Saltillo, Sept. 22, 1848, *Gregg 498* (M); Bofecillos Mts., Sept., 1883, *Havard* (US); Feb. to Oct., 1880, *Ed. Palmer 795* (G, P, US); Cerro de Zapatero, July, 1910, *Purpus 4497* (C, M, US); rocks, near Pena, Feb. 1905, *Purpus* (C).

NUEVO LEON: Monterrey, 1924, *Orcutt 1318* (US).

14. M. intricata T. S. Brandegee in Univ. Calif. Publ. Bot. **4**: 380. 1913; Standl. in Contr. U. S. Nat. Herb. **23**: 1138. 1924. Pl. 4, figs. 7–8; pl. 9, fig. 2.

A branching, erect, subherbaceous perennial, 2.5–4 dm. high; stems opposite or approximate, numerous, divergently branched, conspicuously ribbed, simple below, intricate above, glabrous or rarely sparse-puberulent on the margins of the decurrent petioles; internodes elongated; leaves opposite or becoming approximate above, sessile, few, remote, rudimentary, linear to linear-cuneate, 2–9 mm. long, 0.3–1 mm. broad, acuminate, entire or trifid, sparsely ciliate on the margins, fleshy; flowers rather numerous, terminating the branches of a loosely flowered cyme; pedicels slender, 3–9 mm. long, mostly glabrous, erect in fruit; calyx narrowly turbinate, 4–6 mm. long, mostly glabrous or sparsely hirtellous on the margins of the lobes; calyx-tube short, about 2 mm. long, in anthesis 1–1.5 mm. broad, in fruit 2 mm. broad; lobes 7–11, linear, acuminate, entire, 3–5 mm. long, about 0.3 mm.

broad; corolla shortly infundibuliform, about 10–12 mm. long, golden-yellow; corolla-tube slightly elongated, ampliate, 4–6 mm. long, about 2 mm. broad at the orifice, densely pilose at the base of the throat within; lobes 5–6, oblong-obovate, obtuse, 6–7 mm. long, about 3 mm. broad; stamens exserted, 7–8 mm. long; filaments glabrous, connective inconspicuously prolonged at the apex into a short, acute protuberance; pollen grain minutely and irregularly reticulate, appearing papillate, 62.5–75; (78.75) μ in diameter; pistil 8–10 mm. long; ovules 4 in each cell; stigma slightly capitate; capsule small, about 3 mm. long, twice as broad; seeds 4 in each cell, 2 mm. long, about 1.5 mm. broad, finely and irregularly reticulate, the ridges rather prominent.

Distribution; State of San Luis Potosi, Mexico.

Specimens examined:

MEXICO:

SAN LUIS POTOSI: Minas de San Rafael, May, 1911, *Purpus 5016* (C TYPE, G, NY, US); same locality, July, 1911, *Purpus 5016* (F, G, M, US); same locality, Nov. 1910, *Purpus 5044* (C).

14a. Var. **Purpusii** Steyermark, n. var.[43]

A nearly herbaceous perennial, 0.6–1.2 dm. high, more or less scabrous throughout; leaves 1.5–4 mm. long, 0.3–0.5 mm. broad; corolla 8–10 mm. long, with acute lobes.

Distribution: mountains near Tehuacan, state of Puebla, Mexico.

Specimens examined:

MEXICO:

PUEBLA: mountains, Tehuacan, June, 1905, *Purpus 1318* (C, F, G, M TYPE, NY).

15. M. juncea Harvey, Gen. So. Afr. Pl. ed. 2. 220. 1868; Harvey in Fl. Cap. 4: 484. 1907. Pl. 10, fig. 1.

An erect, paniculately branched, suffruticose perennial, 6–9 dm. high; stems numerous, divaricate, strict, slender, terete, striate, mostly glabrous or minutely puberulent; internodes elong-

[43] Var. **Purpusii** Steyermark, var. nov., subherbacea perennis, 0.6–1.2 dm. alta, plus minusve scabrosa; foliis 1.5–4 mm. longis, 0.3–0.5 mm. latis; corolla 8–10 mm. longa, lobis acutis.—TYPE collected in mountains, Tehuacan, state of Puebla, Mexico, June, 1905, *Purpus 1318* (M).

ated; leaves opposite, sessile, sparse, reduced to mere vestiges, remote, linear, 2–5 mm. long, 1 mm. broad, acute, entire, glabrous or minutely puberulent; flowers relatively numerous in paniculate cymes; pedicels slender, 6–15 mm. long, puberulent, erect in fruit; calyx campanulate, 5–7 mm. long, glabrous or minutely puberulent on the tube and margins of the lobes; calyx-tube 2–3 mm. long; lobes 5, linear, acute, entire, 3–5 mm. long, about 0.75 mm. broad; corolla about 9 mm. long; corolla-tube about 3 mm. long; capsule 6–8 mm. long, 8–10 mm. broad; seeds not seen.

There is a specimen of this species cited in the 'Flora Capensis' as having been collected by Whitehead near Modderfontein in Namaqualand. If this record is correct, then the range of this species should be considerably extended to the western extremity of South Africa.

Distribution: South Africa.

Specimens examined:

AFRICA:

UNION OF SOUTH AFRICA: clearings of Gouritz River, Georg, Karroo, Dec., *Ecklon & Zeyher* (BER, M).

16. M. robusta (Benth.) A. Gray in Am. Jour. Sci. II. **14**: 43. 1852; Walp. Ann. Bot. **5**: 487. 1858; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^2: 14. 1895; Macloskie in Rept. Princeton Univ. Exp. to Patagonia (Bot.) 8^2: 658. 1905. Pl. 4, fig. 3; pl. 10, fig. 2.

Bolivaria robusta Benth. in Hook. London Jour. Bot. **5**: 190. *pl. 5*. 1846.

An erect, divergent, corymbosely branched, spinescent shrub, 6–11 dm. high; stems opposite, rather numerous, ascending, rigid, terete, becoming gradually pungent at the ends of the branches to produce a spinescent condition, covered with numerous, minute warty growths, densely puberulent, fleshy; leaves opposite, sessile, sparse, joined transversely at the base by a suture, reduced on the main branches to small, inconspicuous, cuneate scales, about 1 mm. long, 1–1.5 mm. broad, entire, glabrous, appearing on the short axillary spinescent branches, small, slightly petioled, oblong to linear-obovate, obtuse, entire, densely puberulent, including the petiole, 3–5 mm. long, 1–2 mm. broad; flowers

relatively few, appearing close together at the upper extremities of the main branches, terminal and solitary on the short, slender, axillary branchlets; pedicels densely puberulent, practically sessile, about 2 mm. long; calyx campanulate, 5–6 mm. long; calyx-tube 4 mm. long, about as broad, mostly glabrous; lobes 5–6, deltoid to more or less lanceolate, 2 mm. long, 0.75 mm. broad, entire, acute, puberulent on the margins; corolla infundibuliform, 22–25 mm. long, bright yellow; corolla-tube relatively elongated, about 12 mm. long, 7–8 mm. broad at the orifice, densely pubescent at the base of the throat within; lobes 5–6, ovate, 8–9 mm. long, 6 mm. broad, obtuse, mucronate; stamens exserted, 18–20 mm. long; filaments densely pubescent with short hairs around the base, about 10 mm. long; connective prolonged at the apex into a short, triangular protuberance; pollen grain large, with very large and rather regular reticulations, (66.25); 72.5–81.25; (91.25) μ in diameter; pistil about 25 mm. long; ovules 4 in each cell; stigma slightly capitate; capsule not seen. In regard to the capsule, Bentham says, "Didymous . . . dehiscence, unknown, however."

Distribution: east-central to southern Argentina.

Specimens examined:

South America:

Argentina: Territory Santa Cruz, alt. 50 m., Oct. 14, 1929, *Donat 182* (M); conglomerate uplands, General Roca and vicinity, Rio Negro Valley, alt. 250–360 m., Oct. 20, 1914, *Fischer 28* (US); vicinity of General Roca, Rio Negro, alt. 250–360 m., Sept. 1914–Feb. 1915, *Fischer 28* (C, F, G, NY); Travesia de Rawson á la Cordillera, territorio del Chubut, Nov. 1–30, 1903, *Illin 74* (C).

17. M. spinescens A. Gray in Proc. Am. Acad. **7**: 388. 1867; A. Gray, Syn. Fl. N. Am. 2^1: 78. 1878; Knobl. in Engler & Prantl, Nat. Pflanzenf. 4^3: 14. 1895; Tidestrom in Contr. U. S. Nat. Herb. **25**: 413. 1925; Jepson, Man. Fl. Pl. Calif. 760. 1925.

Pl. 4, figs. 1, 5–6; pl. 11.

An erect, divergent, irregularly branching shrub, 1.5–11 dm. high; stems numerous, stout, terete, slightly furrowed, the lower unarmed, the upper spinose, densely puberulent, the hairs closely

appressed; leaves alternate or fascicled, petiolate, including the petiole, 2–14 mm. long, 0.5–2 mm. broad, entire, fleshy, densely puberulent, the hairs closely appressed, conspicuous, numerous, crowded on the young branches and shoots, less conspicuous, smaller, scale-like or reduced to mere scars on the older and stouter branches, the alternate leaves linear-oblanceolate, acute, the fascicled leaves obovate-spatulate, obtuse or acute; flowers solitary or clustered, very small, numerous, terminating short axillary shoots from the upper parts of the branches; pedicels very short, 2–5 mm. long, glabrous to densely puberulent, erect in fruit; calyx turbinate to campanulate, 4–8 mm. long, glabrous or slightly puberulent; calyx-tube 1–2 mm. long, in anthesis 1–2 mm. broad, in fruit about 2 mm. broad; lobes 5 (rarely 6–8), broadly linear, 3–6 mm. long, about 0.5 mm. broad, obtuse, entire, acute; corolla infundibuliform, 7–9 mm. long, white, tinged brownish-purple without; corolla-tube relatively elongated, more or less abruptly expanded at the orifice, 4–6 mm. long, about 2 mm. broad at the orifice, slightly pubescent with slender short hairs along the length of the throat within; lobes 5, obovate, about 3–3.5 mm. long, 2–2.5 mm. broad, obtuse; stamens only slightly exserted, about 5 mm. long; filaments glabrous, connective not prolonged at the apex; pollen grain small, moderately and regularly reticulate (33.75); 39.9–50 μ in diameter; pistil 5–6 mm. long; ovules 2 in each cell; stigma small, inconspicuous; capsule 5–7 mm. long, 12–14 mm. broad; seeds 2 in each cell, 5–6 mm. long, about 3–4 mm. broad, finely and regularly reticulate.

Distribution: southern and west-central Nevada and adjacent California.

Specimens examined:

The writer has examined numerous mature capsules of this species, but in no instance is there any manifestation of dehiscence. The seeds seem to escape only after the membranaceous pericarp of the cocci, after a period of time, has been broken irregularly in places where punctures of one kind or another have occurred.

Specimens examined:

UNITED STATES:

NEVADA: s. e. part of Nevada, 1865, *Anderson* (G TYPE); Jean,

Clark Co., May, 1915, *K. Brandegee* (C); summit between Basalt and Sand Spring, Esmeralda Co., Sept. 2, 1926, *R. S. Ferris 6678* (DS); Mormon Mts., Lincoln Co., alt. 915–1830 m., July, 1906, *Goodding 134* (C); Amargosa Desert, alt. 915 m., April 16, 1907, *M. E. Jones* (POM); Indian Spring, Charleston Mts., alt. 1403 m., May 7, 1906, *M. E. Jones* (POM); Good Springs, April 30, 1905, *M. E. Jones* (POM); Good Springs, May 1, 1905, *M. E. Jones* (POM); Rhyolite, alt. 1159 m., April 11, 1907, *M. E. Jones* (DS, POM); near Columbus Marsh, June 17, 1927, *M. E. Jones* (POM); Candelaria, June 22, 1882, *M. E. Jones* (POM); Mormon Mts., Lincoln Co., alt. 915–1830 m., July, 1906, *Kennedy & Goodding 134* (NY, US); Sodaville, Mineral Co., *S. B. Parish* (C); sandy soil, palmetto range, alt. 1525–1830 m., May–Oct., 1898, *Purpus 5903* (C, NY, US); Tonopah, alt. 1830 m., May, 1907, *Shockley 106* (C); Candelaria, Mineral Co., *Shockley 17* (C); Candelaria, Mineral Co., May, 1881, *Shockley* (G); base of Mt. Montgomery, near Queen station, alt. 1850 m., June 20, 1919, *Tidestrom 10034* (US); on slopes of the Covillea belt, Goodsprings, alt. 1125 m., April 19, 1919, *Tidestrom 8907* (US); in cañon, Montezuma Mt., near Goldfield, alt. 2100 m., June 4, 1919, *Tidestrom 9775* (US).

CALIFORNIA: Barnwell, May, 1911, *K. Brandegee* (C); Good Springs, May, 1915, *K. Brandegee* (US); Providence Mts., at Fort Mojave, 1860–61, *Cooper* (DS, G); Funeral Mts., Inyo Co., March 21 and 22, 1891, *Coville & Funston 458* (US); Government Holes, Cima Road, 6 mi. from Cima, alt. 1403 m., San Bernardino Co., April 25, 1928, *Ferris 7325* (DS, NY); common at the head of Furnace Creek wash on Death Valley Junction road, Inyo Co., March 17–24, 1924, *Ferris, Scott & Bacigalupi* (DS); Dante's View, Death Valley, May 1, 1927, *Gilman 2* (POM); See Flat, 15 mi. n. of Darwin, Inyo Co., alt. 1586 m., Sept. 28, 1917, *Grinnell* (C); western slope, Argus Mts., Lower Sonoran zone, Inyo Co., alt. 1738.5 m., May 19, 1906, *Hall & Chandler 7096* (C); sand hills west of Laws, Inyo Co., May 8, 1906, *Heller 8202* (DS, F, G, M, NY, P, US); gravelly mesa, Ryan to Shoshone, April 4, 1929, *Hoffmann* (St. B); common in stony washes, Granite Pass, San Bernardino Co., alt. 976 m., May 18, 1930, *Hoffmann* (St. B); sandy flat, 7 mi. s. w. of Darwin, Inyo Co., alt. 1372.5 m., April

27, 1930, *Hoffmann* (St. B.); Funeral Mts., Death Valley region, *Jaeger* (POM); chloride cliff, Funeral Mts., alt. 1220 m., May 8, 1920, *Jaeger 66* (US); Darwin, alt. 1403 m., April 28, 1897, *M. E. Jones* (POM); Cove Spring, Old Dad Mt., May 14, 1926, *M. E. Jones* (POM); 7 mi. e. of Dante's Point, Death Valley region, Inyo Co., alt. 1372.5 m., April 5, 1928, *Munz & Hitchcock 11022* (POM).

17a. Var. mohavensis Steyermark, n. var.[44]

Corolla broadly infundibuliform, 12–15 mm. long; corolla-tube gradually ampliate towards the orifice, 10–12 mm. long; lobes about 4–4.5 mm. long, 3.5–4.5 mm. broad; stamens about 10 mm. long; connective prolonged at the apex into a short, rounded protuberance; pollen grain 43.75–56.25 μ in diameter; pistil 13–14 mm. long; seeds about 7 mm. long, about 5 mm. broad.

Distribution: Mohave Desert of southeastern California.

The characters of the much larger corolla and the more broadly infundibuliform corolla-tube, more ampliate towards the orifice, combined with the limited distribution in the Mohave Desert, seem to warrant treating this as a variety of *M. spinescens*.

Specimens examined:

UNITED STATES:

CALIFORNIA: dry open desert, 13 mi. n. of Barstow, San Bernardino Co., alt. 640.5 m., April 30, 1924, *Fendge 558* (POM); Ordinance Mts., Mohave Desert, Lower Sonoran zone, San Bernardino Co., April 30, 1906, *Hall & Chandler 6780* (C); Funeral Mts., bordering Death Valley, May 15, 1920, *Jaeger 1131* (POM); Calico Mts., Coolgardie Yucca Mesa, Mohave Desert, March 27, 1916, *Jepson 6635* (G); Leastalk, Mohave Desert, San Bernardino Co., June 5, 1915, *S. B. Parish 10360* (DS); plains, Leastalk, Mohave Desert, San Bernardino Co., June 3, 1915, *S. B. Parish 10361* (C); 14 mi. n. e. of Barstow, Mojave Desert, San Bernardino Co., April 23, 1915, *S. B. Parish 9795* (C TYPE, DS); in

[44] Var. **mohavensis** Steyermark, var. nov., corolla late infundibuliformi, 12–15 mm. longa; corollae tubo sensim dilatato 10–12 mm. longo; staminibus circiter 10 mm. longis, connective elongato apice in protuberans breve subglobosum; polline 43.75–56.25μ in diametro; seminibus circiter 7 mm. longis, 5 mm. latis.—TYPE collected 14 miles n.e. of Barstow, Mojave Desert, San Bernardino Co., April 23, 1915, *S. B. Parish 9795* (C).

desert sand, Barstow, Mohave Desert, alt. 640.5 m., April 23, 1921, *Spencer 1776* (G).

SPECIES IMPERFECTLY KNOWN

M. linoides Phil. in Linnaea 33: 173. 1864.

A low, suffruticose, smooth perennial, simulating *Linum aquilinum* Mol. in appearance; leaves slightly exceeding the internodes, opposite, exstipulate, numerous, broadly linear, 10 mm. long, about 2.5 mm. broad, very shortly acuminate, erect, the highest the smallest, bract-like, glabrous, subcoriaceous; flowers few, 1–3, terminal; pedicel 3.1 mm. long; calyx in anthesis 4.2 mm. long, in fruit 6.8–7.3 mm. long, cleft to the middle; lobes 5, narrowly linear, prominently nerved in the middle; corolla light yellow, purplish on the outside, infundibuliform, 14.7 mm. long; corolla-tube short, pilose within; lobes ovate-oblong or ovate; stamens equalling ⅔ of the corolla; filament very long; anthers linear, about 4.2 mm. long; style equalling the stamens; stigma capitate, obscurely 3-lobed; ovules 2 in each cell, erect, paired; mature fruit not present.—TYPE collected between Chincolco and Concumen in the province of Aconcagua, Chile, *Landbeck*.

Compiled from the original description.

M. chlorargantha Remy in Ann. Sci. Nat. Bot. III. 8: 225. 1842.

A branching shrub, about 3 dm. high; stems numerous, slender, dichotomously branched, glabrous; leaves opposite or the highest alternate, slightly petiolate, oblong-lanceolate, 18.5–23 mm. long, about 3.5 mm. broad, entire, acute, glabrous, subcoriaceous; flowers terminal; pedicel 1-flowered; calyx campanulate, glabrous; lobes 6–7, linear, entire, glabrous, obtuse; corolla infundibuliform, twice exceeding the calyx in length, yellowish-white; lobes 6–7, oval-oblong, obtuse; stamens included; anthers ovate; style equalling the stamen in length; stigma capitate, obscurely bi-lobed; seeds 3–4 in each cell, erect, ovate, trigonal.—TYPE collected in hills around Chuquisaca, Bolivia, *d'Orbigny* (Herb. Mus. Paris).

Compiled from the original description.

List of Exsiccatae

The distribution numbers are printed in *italics*. Unnumbered collections are indicated by a dash. The numbers in parentheses are the species number used in this revision.

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Bogusch, E. R. *984* (12).
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Burchell, W. J. *2478*, *2960* (4).
Burtt-Davy, J. *12480* (4); —, *30* (5).
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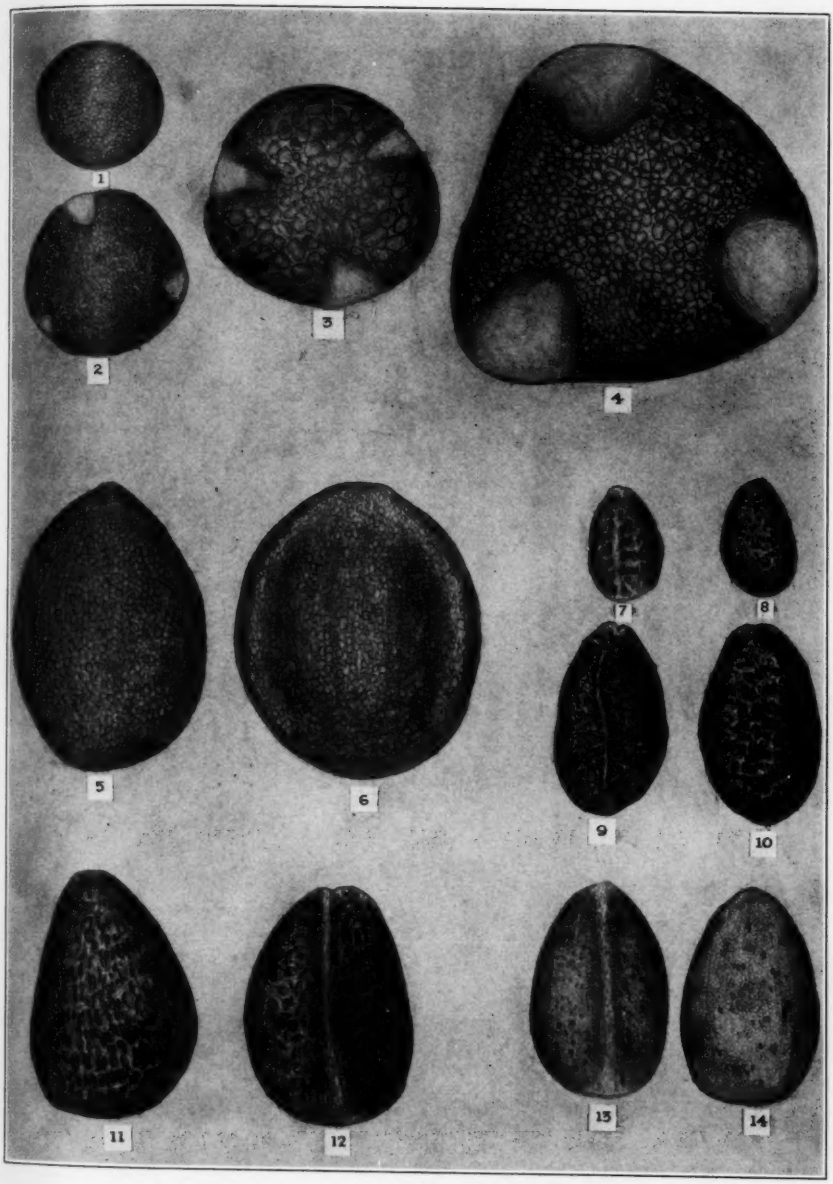
Explanation of Plate

PLATE 4

Fig. 1. Pollen grain of *M. spinescens*, looking down on flat surface. × 180.
Fig. 2. Pollen grain of *M. africana*, looking down on convex surface, showing the three germinal apertures. × 180.
Fig. 3. Pollen grain of *M. robusta*, looking down on convex surface, showing the three germinal apertures. × 180.
Fig. 4. Pollen grain of *M. longiflora*, looking down on convex surface, showing the three germinal apertures. × 180.
Fig. 5. Seed of *M. spinescens*, showing convex outer surface. × 7.
Fig. 6. Same as fig. 5, showing concave inner surface. × 7.
Fig. 7. Seed of *M. intricata*, showing ridge and two flattened faces. × 7.
Fig. 8. Same as fig. 7, showing the convex outer surface. × 7.
Fig. 9. Seed of *M. scoparia*, showing ridge and two flattened faces. × 7.
Fig. 10. Same as fig. 9, showing the convex outer surface. × 7.
Fig. 11. Seed of *M. heterophylla*, showing the convex outer surface. × 7.
Fig. 12. Same as fig. 11, showing ridge and two flattened faces. × 7.
Fig. 13. Seed of *M. scabra*, showing ridge and two flattened faces. × 7.
Fig. 14. Same as fig. 13, showing the convex outer surface. × 7.



STEYERMARK—REVISION OF MENODORA

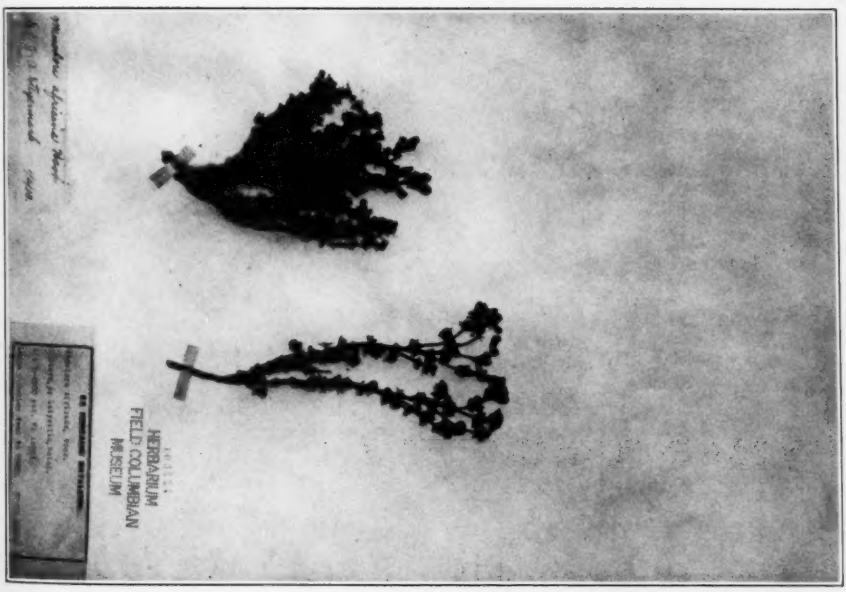
Explanation of Plate

PLATE 5

Fig. 1. *Menodora helianthemoides* HBK. var. *Engelmannii* Steyermark, n. var.
From an authentic specimen, *Ed. Palmer 164*, in the University of California Herbarium.

Fig. 2. *Menodora africana* Hook.
From an authentic specimen, *Wood 7948*, in the Herbarium of the Field Museum of Natural History.

1



2

Explanation of Plate

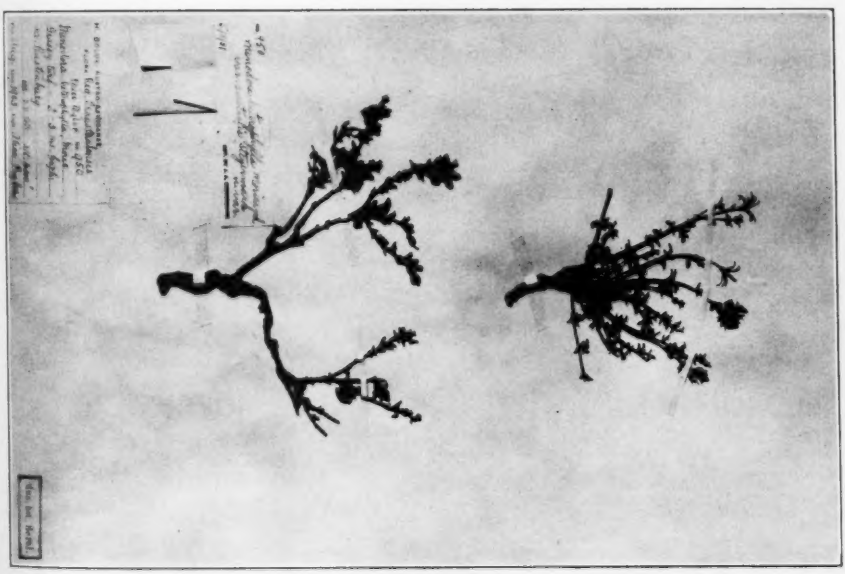
PLATE 6

Fig. 1. *Menodora heterophylla* Moric.

From an authentic specimen, *Reverchon 1328*, in the Herbarium of the Field Museum of Natural History.

Fig. 2. *Menodora heterophylla* Moric. var. *australis* Steyermark, n. var.

From the type specimen, *Pegler 950*, in the Herbarium of the Botanical Garden and Museum of Berlin-Dahlem.



1

STEYERMARK—REVISION OF MENODORA

2

Explanation of Plate

PLATE 7

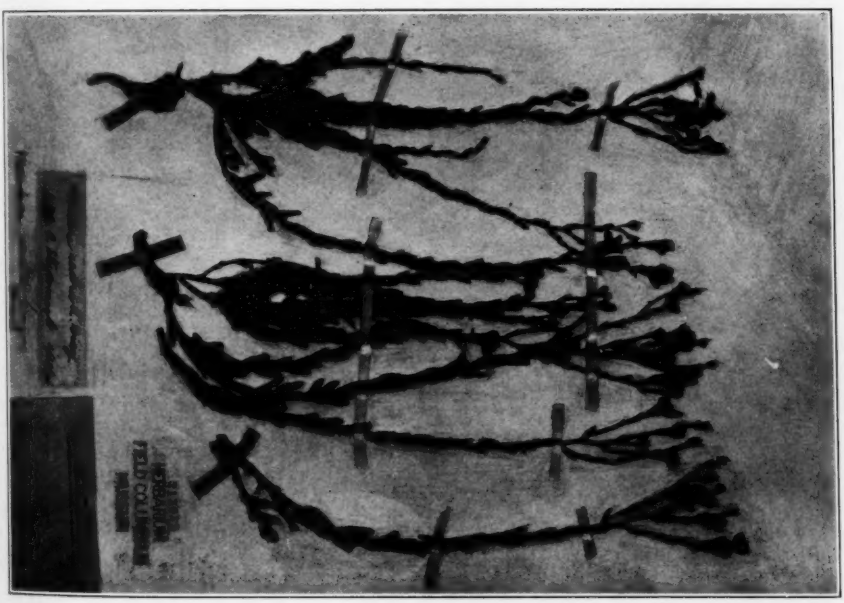
Fig. 1. *Menodora integrifolia* (Cham. & Schlecht.) Steud. var. *trifida* (Cham. & Schlecht.) Steyermark, n. comb.

From an authentic specimen, *Hassler 6475*, in the Gray Herbarium of Harvard University.

Fig. 2. *Menodora scabra* A. Gray.

From an authentic specimen, *Ed. Palmer 309*, in the Herbarium of the Field Museum of Natural History.

1



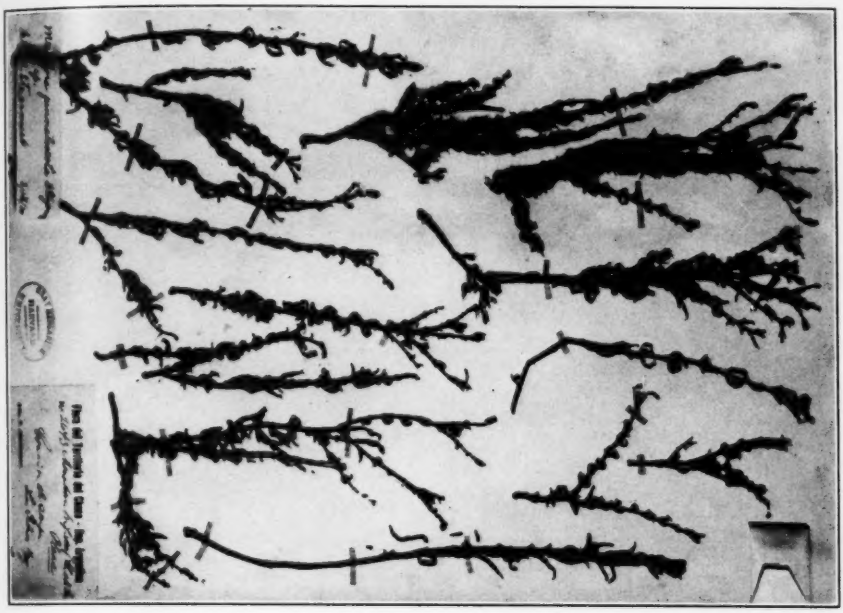
2

Explanation of Plate

PLATE 8

Fig. 1. *Menodora pinnatisecta* Steyermark, n. sp.
From the type specimen, *Jörgensen 2643*, in the Gray Herbarium of Harvard University.

Fig. 2. *Menodora decemfida* (Gill.) A. Gray.
From an authentic specimen, *Fielding*, in the Gray Herbarium of Harvard University.



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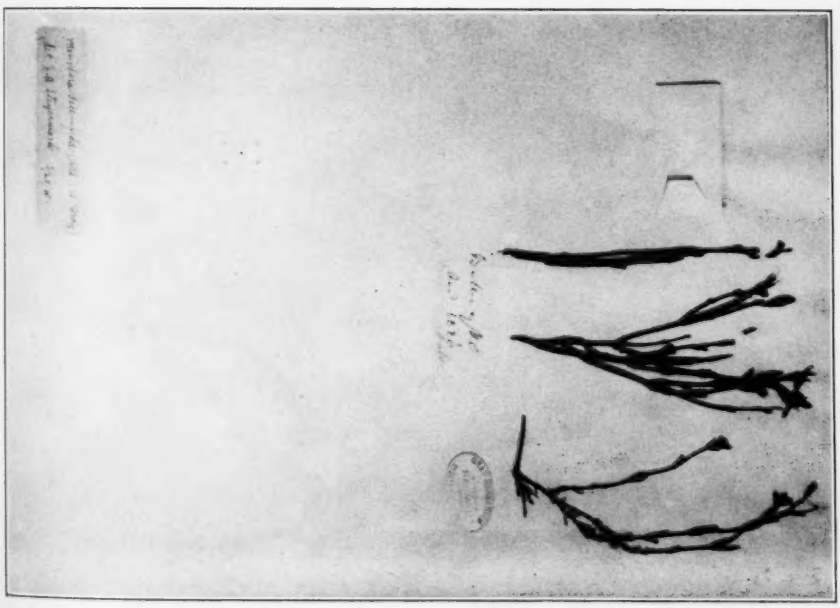


2

Explanation of Plate

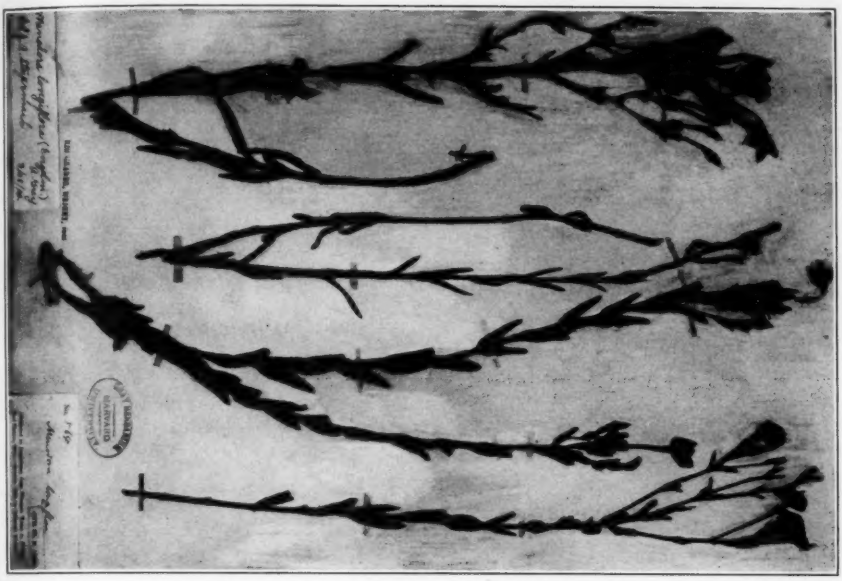
PLATE 9

Fig. 1. *Menodora longiflora* (Engelm.) A. Gray.

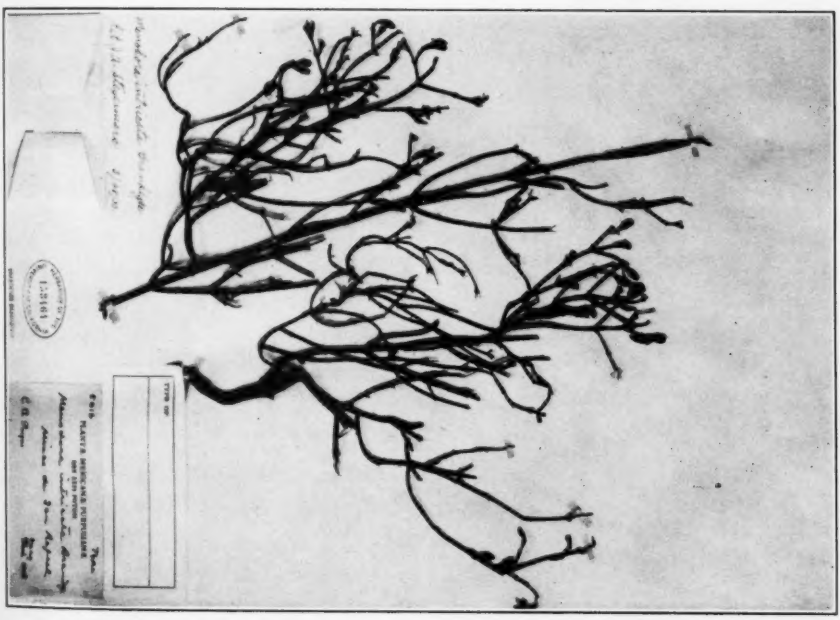
From an authentic specimen, *Wright 564*, in the Gray Herbarium of Harvard University.

Fig. 2. *Menodora intricata* Brandegee.

From the type specimen, *Purpus 5016*, in the Herbarium of the University of California.



1



2

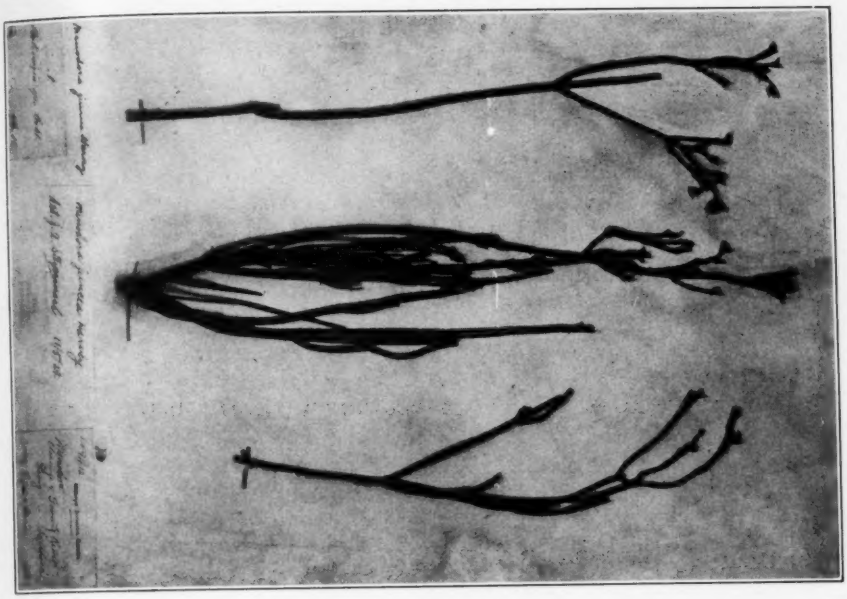
STEYERMARK—REVISION OF MENODORA

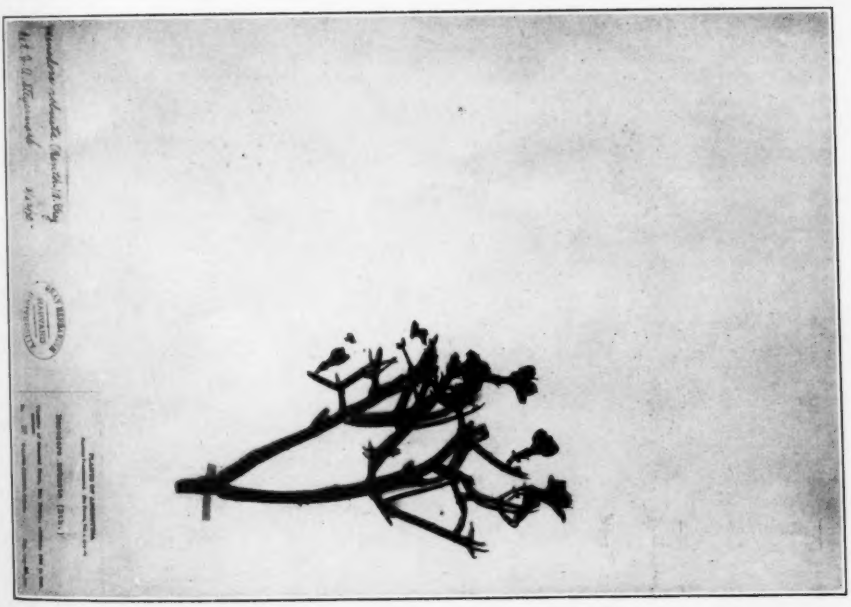
Explanation of Plate

PLATE 10

Fig. 1. *Menodora juncea* Harvey
From an authentic specimen, *Ecklon & Zeyher "94.12"* in the Herbarium of the Missouri Botanical Garden.

Fig. 2. *Menodora robusta* (Benth.) A. Gray
From an authentic specimen, *Fischer 28*, in the Gray Herbarium of Harvard University.





Explanation of Plate

PLATE 11

Menodora spinescens A. Gray

From an authentic specimen, *K. Brandegee*, in the Herbarium of the University of California.

STEYERMARK—REVISION OF MENODORA